Journal of the Fisheries Research Board of Canada

Journal de l'office des recherches sur les pêcheries du Canada

Volume 33, No. 2, February 1976

Volume 33, nº 2, février 1976

Environment Canada
Fisheries and Marine Service

Environnement Canada
Service des pêches et des sciences de la mer

Journal of the Fisheries Research Board of Canada

Journal de l'office des recherches sur les pêcheries du Canada

Environment Canada
Fisheries and Marine Service
Office of the Editor

Environnement Canada
Service des pêches et des sciences de la mer
Bureau du Rédacteur

116 Lisgar, Ottawa K1A 0H3

Volume 33, No. 2, February 1976

Volume 33, nº 2, février 1976

The *Journal of the Fisheries Research Board of Canada* has been published continuously since 1901, previously as *Contributions to Canadian Biology* 1901–25, *Contributions to Canadian Biology and Fisheries* 1926–34, and *Journal of the Biological Board of Canada*, 1934–37.

Editorial policy — The *Journal* publishes original research articles and notes, critical reviews, essays of opinion or hypothesis, letters, and book reviews in the broad field of fisheries management, ocean science, and aquatic environments relevant to Canada. Submissions in English or French are accepted without limitations as to origin, but must not have been published or copyrighted and must not be published elsewhere except in abstract form or by written consent of the Editor. The *Journal* accepts no responsibility for statements made by contributors. Details on submissions are given in guides to authors and typists at the back of this issue. Reprints of these guides are available free from the Office of the Editor.

A charge of $40.00 per page is made for manuscripts published. When submitting a manuscript, an author must state that the charge will be accepted.

Subscriptions — The *Journal* is issued monthly to form annual volumes of twelve numbers. Subscription rates are: Canada, $30.00 per year; other countries, $36.00. Single issues are $3.00 and $3.75, respectively. Orders must be sent directly to Information Canada, Ottawa, Canada K1A 0S9, and payment made in Canadian funds to "The Receiver General for Canada."

Microfilm — Issues from 1934 through the current volume can be purchased on 16 or 35 mm microfilm. Photocopies of individual articles or issues can be purchased. Address orders to Xerox University Microfilms, 300 North Zeeb Road, Ann Arbor, Michigan 48106, USA.

Publié depuis 1901, le *Journal de l'office des recherches sur les pêcheries du Canada* a paru sous plusieurs titres: *Contributions to Canada Biology*, 1901–25, *Contributions to Canadian Biology and Fisheries*, 1926–34, et *Journal of the Biological Board of Canada*, 1934–37.

Politique de publication — Le *Journal* publie des articles de recherches, ainsi que des notes, critiques, exposés d'opinions ou d'hypothèses, lettres et recensions concernant le vaste domaine de la gestion des pêches, des sciences de la mer et des milieux aquatiques au Canada. Toutes contributions en français ou en anglais sont acceptées sans restriction quant à la provenance, mais elles ne doivent pas avoir été produites ni avoir fait l'objet d'un copyright et ne doivent pas être publiées nulle part ailleurs sauf sous forme abrégée ou avec le consentement écrit du directeur. Le *Journal* décline toute responsabilité pour ce qui est des affirmations des collaborateurs. Les modalités de présentation des textes font l'objet du guide des auteurs et du guide des dactylos paraissant à la fin du présent numéro. On peut se procurer gratuitement, du bureau du directeur, des exemplaires de ces guides.

Les frais de publication sont de $40.00 la page. Quant un auteur présente un texte, il doit préciser que ces frais seront acceptés.

Abonnement — Le *Journal* parait tous les mois, formant ainsi un volume de 12 numéros par année. Les frais d'abonnement annuel sont de $30 pour le Canada et de $36 pour les autres pays. Chaque numéro coûte $3.00 au Canada et $3.75 à l'étranger. Prière d'adresser directement les commandes à Information Canada, Ottawa (Ontario), Canada K1A 0S9; les paiements doivent être faits en devises canadiennes, à l'ordre du Receveur général du Canada.

Microfilms — On peut acheter sur microfilms 16 ou 35 mm tous les numéros publiés depuis 1934. Des photocopies d'articles ou de numéros individuels sont aussi en vente. Prière d'adresser les commandes à Xerox University Microfilms, 300 North Zeeb Road, Ann Arbor, Michigan 48106, E.-U.

Editor and Director of Scientific Information/ Rédacteur et Directeur de l'information scientifique — J. C. STEVENSON, PH.D.

Deputy Editor/ Sous-rédacteur — J. WATSON, PH.D.

Assistant Editors/ Rédacteurs adjoints — JOHANNA M. REINHART, M.SC., D. G. COOK, PH.D.

Assistant to the Editor/ Adjointe au rédacteur — NATALIE SUTTERLIN

Production-Documentation — J. CAMP/G. NEVILLE/PAULA IRVING

French Abstracts/ Résumés français — Y. JEAN, PH.D.

Journal of the Fisheries Research Board of Canada

Journal de l'office des recherches sur les pêcheries du Canada

Volume 33, No. 2, February 1976

Volume 33, n° 2, février 1976

Preferred Temperatures of F_3 to F_5 Hybrids of *Salvelinus fontinalis* × *S. namaycush*

C. I. GODDARD AND J. S. TAIT

Department of Biology, York University, Downsview, Ont. M3J 1P3

GODDARD, C. I., AND J. S. TAIT. 1976. Preferred temperatures of F_3 to F_5 hybrids of *Salvelinus fontinalis* × *S. namaycush*. J. Fish. Res. Board Can. 33: 197–202.

Preferred temperatures were determined for samples of four generations, F_3, F_4, "$F_{4\text{-}5}$" ($F_4 \times F_3$), and F_5 of yearling splake (*Salvelinus fontinalis* × *S. namaycush*), acclimated 4, 8, 12, 16, and 20 C. Final preferenda for the four generations were 16.3, 15.9, 15.7, and 14.8 C, respectively, decreasing as generation number increased. Although these values are close to the 16 C preferendum of *S. fontinalis*, they show a trend towards the lake trout preferendum of 11.7 C. The hybrids are like *S. namaycush* in having preferred temperatures that are virtually unaffected by changes in acclimation temperature or season.

GODDARD, C. I., AND J. S. TAIT. 1976. Preferred temperatures of F_3 to F_5 hybrids of *Salvelinus fontinalis* × *S. namaycush*. J. Fish. Res. Board Can. 33: 197–202.

Nous avons déterminé les températures préférées d'échantillons de quatre générations, F_3, F_4, « $F_{4\text{-}5}$ » ($F_4 \times F_3$) et F_5 de truites moulac (*Salvelinus fontinalis* × *S. namaycush*) de l'année, acclimatées à 4, 8, 12, 16 et 20 C. Les températures préférées finales pour les quatre générations sont 16.3, 15.9, 15.7 et 14.8 respectivement, décroissant d'une génération à l'autre. Alors que ces valeurs se rapprochent de la température préférée (16 C) de *S. fontinalis*, elles marquent une tendance vers le preferendum de 11.7 C du touladi. Les hybrides ressemblent à *S. namaycush* en ceci que leurs températures préférées sont pratiquement indépendantes des changements de température d'acclimatation ou de la saison.

Received December 31, 1974
Accepted October 28, 1975

Reçu le 31 décembre 1974
Accepté le 28 octobre 1975

THE purpose of this study was to determine in the laboratory the preferred temperatures of several generations of brook trout (*Salvelinus fontinalis*) × lake trout (*S. namaycush*) hydrids, commonly called splake. Although the hybrid was first produced almost a century ago and has been stocked sporadically across Canada and northern United States, there is little published information about its temperature distribution in natural waters and there are no published accounts of laboratory determinations of preferred temperature. However, an unpublished report by Pearson (1952) of preferred temperature studies on F_1 hybrids indicated a preferendum of about 12 C, similar to that of lake trout. Field observations (Budd 1957; Martin and Baldwin 1960) suggested that the hybrids frequent somewhat

Printed in Canada (J3685)
Imprimé au Canada (J3685)

warmer water in summer than might have been predicted from Pearson's laboratory study.

In anticipation of extensive information on depth and temperature distribution of the hybrids being planted in Lake Huron by the Ontario Ministry of Natural Resources, there was considerable interest in doing further laboratory studies of preferred temperature of the hybrid. It was also of interest to establish the position of the preferred temperature of the hybrids in relation to that of the two parent species and to look for possible shifts in preferred temperature that might have occurred through several generations of selective breeding for other characters.

When the study was begun, the generations available were F_3, F_4, "$F_{4.5}$" (progeny of $F_4 \times F_3$), and F_5. Although desirable for a more complete picture of inheritance patterns, F_1 and F_2 stocks were not available. However, the samples that were tested, coming from higher generations, better represent the hybrids currently being planted.

Materials and Methods

The fish used in this investigation were obtained from stocks of the Selective Breeding Unit, Ministry of Natural Resources, Maple, Ontario. The F_1 hybrid progenitors of these stocks had been produced by fertilizing lake trout eggs with brook trout sperm, and the intervening generations from F_2 onward had been subjected to selection for retention of swimbladder gas and for early maturity (Tait 1970). For each generation to be tested, a few fish were taken from each of several available families to make up a sample of at least 30 fish. Thus samples were as representative of generations as possible but at best were rather narrowly based.

The samples of F_4, "$F_{4.5}$," and F_5 hybrids were obtained first and were acclimated and tested successively at 4, 8, 12, 16, and 20 C during the period from May to November 1971. The sample of F_3 hybrids came from a year-class 1 yr younger. They were acclimated and tested at the same temperatures as the others but during the period from October 1971 to April 1972. Hence they were approximately 6 mo younger than the other generations during testing. They were just under 1 yr when their testing was begun. With this exception all observations were made on yearling fish. The mean lengths and weights of the samples during the experiments were as follows:

	Length (*mm*)		Weight (*g*)	
Generation	Mean	SD	Mean	SD
F_3	97.7	19.9	10.6	4.8
F_4	132.0	14.9	21.4	8.0
"$F_{4.5}$"	131.3	14.0	22.8	8.4
F_5	137.2	15.8	26.1	9.4

The fish were acclimated in 100-liter cylindrical tanks continuously supplied with charcoal-filtered, aerated Toronto tap water. Acclimation temperatures were raised 1 C/day up to the desired temperature. Then the temperature was held constant for at least 3 wk. The temperature regulating apparatus was mounted directly above the acclimation tanks and consisted of two tanks, a 1-hp Min-o-Cool refrigeration unit, and a thermistor-relay-heater system. The temperature was monitored daily and it seldom varied more than ±0.1 C. When higher temperatures were required, the water supply was warmed by a series of 750-W flow-through heaters. The fluorescent lights in the room were controlled by a Tork time switch which was adjusted biweekly to maintain normal photoperiod. All of the tests at each acclimation temperature were performed as close together in time as could be arranged, usually within a period of 2 wk.

The vertical temperature gradient tank was similar to those used by Brett (1952) and McCauley and Tait (1970). The dimensions of the tank were 90 × 90 × 50 cm and the capacity was 405 liters. The glass front was marked off into 10 horizontal zones by parallel lines 8 cm apart, and a thermometer was inserted into each zone through the right side of the tank.

When not in use, the gradient tank was kept filled with aerated water at 3 C. To establish a linear thermal gradient, 50 C water was run through an aluminum heating coil from top to bottom. Water at 0 C was circulated through a cooling coil at the bottom of the tank to maintain the colder temperatures. While the gradient was being established, eight fish, selected at random from the sample being tested, were placed in the tank. The room was dimly lit by four fluorescent lights, producing incident light of 35 lx on the front of the tank.

Observations of the "instantaneous" distribution of the fish within the 10 zones were made every 30 s for 10 min. The resulting set of 160 observations (8 fish × 20 locations) was called a "run." The mean temperature of each zone was determined from thermometer readings taken just before and after each run. During a run the temperature in a zone seldom varied more than ±0.1 C. When one run was completed, the gradient was altered and another run was begun. Ten runs were done per day. The eight fish were removed to a separate holding tank and were not used again at that acclimation temperature. Thirty runs were carried out for each generation at each acclimation temperature. For each run, a mean preferred temperature was calculated from the temperature frequency distribution. Thus, the preferred temperature of each generation at each acclimation was based on the response of 24 randomly chosen fish, and the final preferendum for each generation was based on 24,000 observations. The statistical tests used in this paper were applied to the mean preferred temperatures of the runs rather than to the original observations. Analysis of variance and the Student–Newman–Keuls multiple range test (Woolf 1968) were used for detection of statistically significant effects.

TABLE 1. Preferred temperatures of four generations of splake at five acclimation temperatures.

Generation	Acclimation temperature (C)	Preferred temperature as the mean of means of 30 runs (C)	Final preferendum (C)	Mean preferendum (C)
	4	15.4 ± 0.07[a]		
	8	16.2 ± 0.08		
F_3	12	16.3 ± 0.05	16.3	16.2 ± 0.06[a]
	16	16.4 ± 0.07		
	20	16.2 ± 0.07		
	4	15.7 ± 0.10		
	8	15.9 ± 0.15		
F_4	12	16.7 ± 0.07	15.9	16.1 ± 0.10
	16	16.1 ± 0.14		
	20	15.8 ± 0.07		
	4	15.5 ± 0.07		
	8	15.8 ± 0.15		
"$F_{4.5}$"	12	15.7 ± 0.23	15.7	15.7 ± 0.10
	16	15.7 ± 0.15		
	20	15.8 ± 0.05		
	4	14.6 ± 0.07		
	8	15.3 ± 0.12		
F_5	12	14.7 ± 0.14	14.8	14.9 ± 0.09
	16	14.8 ± 0.14		
	20	14.8 ± 0.14		

[a]1 SD of the mean.

Results

When splake were presented with a temperature gradient spanning about 14 C, they distributed themselves most of the time over a relatively narrow part of the range. The temperature frequency distributions of typical runs had standard deviations of 1.2–2.0 about the mean. When the mean of means is used to express preferred temperature, the values for the splake samples tested fall between 14.6 and 16.7 C (Table 1). The curves formed by plotting these preferred temperatures for each generation against acclimation temperature (Fig. 1) are practically horizontal straight lines, indicating that preferred temperature is unaffected by acclimation temperature. The final preferenda (Table 1) determined by the intersection of these curves with the 45° line in Fig. 1 (Fry 1947) appear to decrease as generation number increases from F_3 to F_5. To test whether the differences between generations are significant, comparisons could be made at each acclimation temperature. However, since acclimation appears to have little effect on preferred temperature of these hybrids, means from the five acclimation temperatures were combined to calculate a mean of means for each generation, listed as mean preferendum in Table 1. The mean preferenda are almost the same numerically as the corresponding final preferenda but they make statistical comparisons among generations possible. The differences among generation means were significant ($P < 0.01$). The results of the multiple range test are summarized as follows:

F_5	"$F_{4.5}$"	F_4	F_3
14.86	15.74	16.08	16.17

The difference between the F_3 and F_4 means is not significant, signified by underlining. In each of the other five comparisons between means the difference is highly significant ($P < 0.01$).

The behavior of the hybrids in the gradient tank was intermediate to that of lake trout and brook trout observed in concurrent preferred temperature experiments (Goddard and Tait 1975). The hybrids were more aggressive than lake trout, which showed little interaction and tended to group themselves into two or three zones, but they were less aggressive and more tightly grouped than brook trout, which swam more actively and were scattered through four or five zones. The hybrids appeared to be less aggressive as generation number increased.

Discussion

The final temperature preferenda of F_3 to F_5 generation hybrids are higher than those of F_1 hybrids and lake trout. They are the same as or

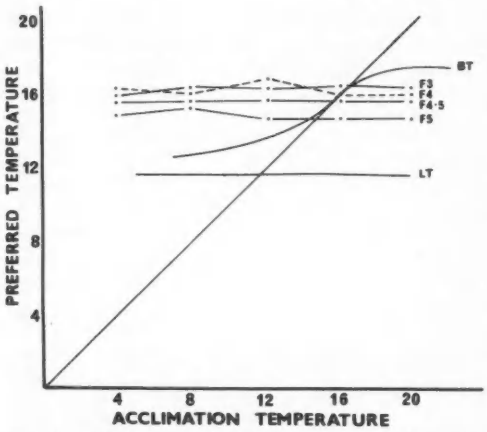

FIG. 1. Relation of preferred temperature to acclimation temperature in hybrids of brook trout (*Salvelinus fontinalis*) × lake trout (*S. namaycush*). Curves for parent species are shown for comparison. The brook trout (BT) curve is based on Graham (1948), the lake trout (LT) on McCauley and Tait (1970).

slightly lower than that of brook trout. F_1 hybrids were reported by Pearson (1952) to have a final preferendum of "approximately 12 C." Inspection of her plotted data yielded a technical value of 11.7 C, the same as the final preferendum of lake trout (McCauley and Tait 1970). The higher generations of hybrids have final preferenda (Table 1) that are 3.1–4.6 C higher than that of lake trout. These values are in the lower half of the 14–18 C range stated as the final preferendum of brook trout by Graham (1948). He stated the preferendum as a range because his preferred temperature–acclimation temperature curve is sigmoid with the middle portion following the 45° line rather than sharply intersecting it (Fig. 1). Examining his data, we conclude that the best interpretation is a final preferendum of 16 C. Our study of seasonal effects on brook trout and lake trout (Goddard and Tait 1975) do not yield final preferenda for comparison here because acclimation temperature was constant.

While F_3 to F_5 hybrids have final preferenda near that of brook trout, obviously they are like lake trout in showing no change in preferred temperature when acclimation temperature is varied. Similarly, Pearson's F_1 hybrids showed no change in preferred temperature when tested at six acclimation temperatures.

There is no evidence of a seasonal effect on the preferred temperature of splake. Although none of the generations was tested over a full year the F_3 generation was tested from October to April and the others from May to November. In all cases acclimation temperatures were being increased as the seasons progressed, and, as already noted (Fig. 1), preferred temperatures did not change. It is unlikely that seasonal and acclimation effects exactly cancelled each other. The fish tested in winter, F_3 generation, had a higher preferred temperature than those tested in summer, "$F_{4.5}$" and F_5 generations. The reverse would have been expected if the hybrids had behaved like brook trout, which have a lower preferred temperature in winter than in summer (Sullivan and Fisher 1953; Goddard and Tait 1975). The evidence here is that the hybrids are like lake trout, which show no seasonal change in preferred temperature (Goddard and Tait 1975).

Although there is some indication in these samples of a negative correlation between mean preferred temperature and body weight, it is unlikely that preferred temperature is dependent on size differentials of the magnitude present here.

The significant differences in mean preferred temperature among generations indicate a downward trend. The decrease of 1.3 C in mean preferred temperature between F_3 and F_5 generations without deliberate selection for temperature characteristics is a benefit for Ontario's splake breeding program, if our somewhat narrowly based samples are typical of hybrids being planted. A low preferred temperature, near that of lake trout, is consistent with the original objectives of the program to produce a strain of early-maturing hybrids capable of living in deep water (Tait 1970). Ability to swim deep would not by itself guarantee exploitation of abundant prey species that live in deep water, if a preference for warmer water kept the predators in the thermocline during summer.

Valuable comparisons can be made between the laboratory data and field observations on the temperature distribution of splake.

F_1 hybrids, as noted earlier, appear to live in somewhat warmer water in lakes in summer than might be predicted from Pearson's 12 C laboratory preferendum. Their distribution is between those of lake trout and brook trout. Clearly, they are in warmer shallower water than lake trout are under similar circumstances but their warm temperature avoidance level is lower than that of brook trout. For example, Budd (1957) reported that F_1 hybrids in South Bay, Lake Huron "did not go as deep as the lake trout and were taken in depths of from 8 to 12 fath or in the region of the thermocline." Martin and Baldwin (1960) found that in Algonquin Park lakes most of the F_1 hybrids were in the 8–20 C temperatures of the thermocline during summer stratification. A calculation based on data from Martin and Bald-

win's fig. 1 gave an approximate value of 14 C as the mean temperature at which splake were caught in Jack Lake in the summers of 1955 and 1957. Other field studies of F_1 splake suggest an avoidance of warm water at temperatures close to or slightly higher than those avoided by lake trout. In Parvin Lake, Colorado, F_1 splake moved into deeper cooler water when surface temperatures exceeded 15.5 C (Burkhard 1962). Migration out of Parvin Lake into an inlet stream reached a peak just after the lake surface warmed to 16 C and while minimum stream temperatures were in the 4–13 C range (Klein 1966).

F_2 hybrids in a thermally stratified lake show maximum genetic segregation for preferred temperature by occupying a range of temperatures that includes the low end of the lake trout range and the high end of the brook trout range. In a depth distribution study by Straight (1969) they tolerated a temperature range of 5–22 C. In July, their peak density was near 18 C in the thermocline but a large proportion of them were caught at 5 C in the hypolimnion. In August and September, their peak density was in the 7–12 C range. Straight points out that their range of peak density in late summer was intermediate to that of lake trout (5–6 C) and of brook trout (12–20 C) in the same lake.

F_4 and F_5 hybrids of a selected strain planted in Lake Huron provide the most appropriate field data for comparison with our laboratory measurements of temperature preferenda. In summer, they appear to remain below 16 C, indicating that there may have been selection for temperature that has contracted their temperature range and shifted the preferred temperature downward. Preliminary data are available from annual reports by Spangler (1971, 1972). Of 430 splake netted in South Bay, Lake Huron in the summers of 1970 and 1971, 82% were in the 8–15.9 C range and the mean temperature at which they were caught was 11.8 C. Field observations by Berst and Payne (1974) suggest avoidance of cold temperatures by F_4 and F_5 splake. Those planted in early spring in 2–3 C water off the southern shore of Georgian Bay tended to move into nearby streams at 7 C. However, those planted later when the lake was at 6.5–8.5 C and streams at 13–15 C appeared to stay out of the streams.

The preferenda for F_3 to F_5 hybrids conform to the pattern observed by Ferguson (1958) that laboratory determinations of temperature preferenda of fish usually are higher than field results. The F_4 and F_5 hybrids have laboratory preferenda that are about 3 C above their mean temperature distribution in South Bay. In lake trout, the difference is about 2 C (McCauley and Tait 1970). In brook trout, thermal preferences in lake and aquarium are similar (Graham 1948). Existing evidence suggests that F_1 hybrids go against the general pattern by having a laboratory preferendum about 2 C below the mean distribution in the field.

Thus, while observations in both field and laboratory appear to show that preferred temperature of higher generations of hybrids is moving towards that of lake trout, a difference of 2 or 3 C still remains. If the trend indicated by our observations continues, a 12 C preferendum might be reached in three or four more generations. However, this goal probably will be reached more rapidly through the current procedure of backcrossing the selected hybrid strain to lake trout.

The observations reported here show that, without deliberate selection for temperature characteristics, preferred temperature of trout hybrids has been changed in three generations. This implies that it may be relatively easy to breed selectively for strains of fish with particular temperature traits within the limits set by the genetic material of parent stocks. In the present case a strain of hybrids preferring to live in the cold water of the hypolimnion and a strain preferring the warm water of the upper thermocline or the epilimnion are possible within the temperature ranges of the parent species.

Acknowledgments

We thank G. Howard for help in recording and processing data; F. Burrows and G. Temple for technical assistance; Dr P. Ihssen, Ontario Ministry of Natural Resources for fish stocks; and the Province of Ontario for a graduate fellowship to C.I.G.

BERST, A. H., AND N. R. PAYNE. 1974. Stream migrations of yearling splake (*Salvelinus fontinalis* × *S. namaycush*) planted in Georgian Bay. J. Fish. Res. Board Can. 31: 226–229.

BRETT, J. R. 1952. Temperature tolerance in young Pacific salmon, genus *Oncorhynchus*. J. Fish. Res. Board Can. 9: 265–323.

BUDD, J. C. 1957. Introduction of the hybrid between the eastern brook trout and lake trout into the Great Lakes. Can. Fish. Cult. 20: 25–28.

BURKHARD, W. T. 1962. A study of the splake trout in Parvin Lake, Colorado. M.Sc. Thesis. Colorado State Univ., Fort Collins, Colo. 77 p.

FERGUSON, R. G. 1958. The preferred temperature of fish and their midsummer distribution in temperate lakes and streams. J. Fish. Res. Board Can. 15: 607–624.

FRY, F. E. J. 1947. Effects of the environment on animal activity. Univ. Toronto Stud., Biol. Ser. 55, Pub. Ont. Fish. Res. Lab. 68: 62 p.

GODDARD, C. I., and J. S. TAIT. 1975. Seasonal effects on preferred temperatures of brook trout, *Salvelinus fontinalis*, and lake trout, *S. namaycush*. Can. J. Zool. (In press)

GRAHAM, J. M. 1948. Some relations of temperature and

oxygen to the activity of the speckled trout *Salvelinus fontinalis* (Mitchill). M.A. Thesis. Univ. Toronto, Toronto, Ont. 47 p.

KLEIN, W. D. 1966. The summer movement of hybrid and brook trout into an inlet stream. Prog. Fish Cult. 28: 146–151.

MARTIN, N. V., AND N. S. BALDWIN. 1960. Observations on the life history of the hybrid between eastern brook trout and lake trout in Algonquin Park, Ontario. J. Fish. Res. Board Can. 17: 541–551.

MCCAULEY, R. W., AND J. S. TAIT. 1970. Preferred temperature of yearling lake trout, *Salvelinus namaycush*. J. Fish. Res. Board Can. 27: 1729–1733.

PEARSON, B. E. 1952. The behavior of a sample of hybrid trout (*Salvelinus fontinalis* × *Cristivomer namaycush*) in a vertical temperature gradient. MS Rep. Great Lakes Inst. Library, Univ. Toronto, Toronto, Ont. 24 p.

SPANGLER, G. R. 1971. Lake Huron Unit: splake, p. 47–49. *In* Research review 70. Ont. Dep. Lands For.

1972. Lake Huron unit: splake, p. 27–29. *In* Research review 71. Ont. Minist. Nat. Resour.

STRAIGHT, W. J. 1969. Depth distribution of splake of known ability to retain swimbladder gas. M.Sc. Thesis. York Univ., Downsview, Ont. 45 p.

SULLIVAN, C. M., AND K. C. FISHER. 1953. Seasonal fluctuations in the selected temperature of speckled trout, *Salvelinus fontinalis* (Mitchill). J. Fish. Res. Board Can. 10: 187–195.

TAIT, J. S. 1970. A method of selecting trout hybrids (*Salvelinus fontinalis* × *S. namaycush*) for ability to retain swimbladder gas. J. Fish. Res. Board Can. 27: 39–45.

WOOLF, C. M. 1968. Principles of biometry. D. Van Nostrand Company Inc., Princeton, N.J. 359 p.

Acute Toxicity of Sodium Chloride, Pentachlorophenol, Guthion®, and Hexavalent Chromium to Fathead Minnows (*Pimephales promelas*) and Goldfish (*Carassius auratus*)[1]

IRA R. ADELMAN, LLOYD L. SMITH JR., AND GARY D. SIESENNOP

Department of Entomology, Fisheries, and Wildlife, University of Minnesota, St. Paul, Minn. 55108, USA

ADELMAN, I. R., L. L. SMITH JR., AND G. D. SIESENNOP. 1976. Acute toxicity of sodium chloride, pentachlorophenol, Guthion®, and hexavalent chromium to fathead minnows (*Pimephales promelas*) and goldfish (*Carassius auratus*). J. Fish. Res. Board Can. 33: 203–208.

The 96-h LC50's for sodium chloride were 7650 and 7341 mg/liter, for pentachlorophenol 0.21 and 0.22 mg/liter, for Guthion® 1.9 and 2.4 mg/liter, and for hexavalent chromium 48 and 120 mg/liter, for fathead minnows (*Pimephales promelas*) and goldfish (*Carassius auratus*), respectively. Threshold LC50's were reached in 6 days for sodium chloride (7650 and 7322 mg/liter for fathead minnows and goldfish, respectively), and pentachlorophenol (0.21 and 0.21 mg/liter), but were not attained in 11 days (termination of testing) with Guthion® (0.76 and 0.80 mg/liter) and hexavalent chromium (18 and 33 mg/liter). With pentachlorophenol and Guthion® goldfish were initially more resistant, but by termination there was no significant difference in LC50's between the two species. With hexavalent chromium the goldfish were more resistant throughout the 11-day test, and with sodium chloride goldfish were initially more resistant but at attainment of a threshold LC50 were less resistant. Use of toxicity curves for assessment of acute mortality permits interpretation not possible in 96-h tests where LC50's are computed at 24-h intervals.

ADELMAN, I. R., L. L. SMITH JR., AND G. D. SIESENNOP. 1976. Acute toxicity of sodium chloride, pentachlorophenol, Guthion®, and hexavalent chromium to fathead minnows (*Pimephales promelas*) and goldfish (*Carassius auratus*). J. Fish. Res. Board Can. 33: 203–208.

Les CL50 après 96 h de chlorure de sodium sont de 7650 et 7341 mg/litre, de pentachlorophénol 0.21 et 0.22 mg/litre, de Guthion® 1.9 et 2.4 mg/litre, et de chrome hexavalent 48 et 120 mg/litre pour les têtes-de-boule (*Pimephales promelas*) et les poissons dorés (*Carassius auratus*) respectivement. Les CL50 de seuil sont atteintes en 6 jours pour le chlorure de sodium, 7650 et 7322 mg/litre, et pour le pentachlorophénol, 0.21 et 0.21 mg/litre, avec les têtes-de-boule et les poissons dorés respectivement, mais ne sont pas encore atteintes après 11 jours (fin des essais) pour le Guthion®, 0.76 et 0.80 mg/litre, et pour le chrome hexavalent, 18 et 33 mg/litre. Avec le pentachlorophénol et le Guthion®, les poissons dorés sont plus résistants au début, mais à la fin des essais il n'y a pas de différence significative de CL50 entre les deux espèces. Avec le chrome hexavalent, les poissons dorés sont plus résistants sur toute la durée de l'expérience de 11 jours. Avec le chlorure de sodium, les poissons dorés montrent une plus grande résistance initiale, mais une fois atteinte une CL50 de seuil, sont moins résistants. L'emploi de courbes de toxicité pour l'évaluation de la mortalité aiguë permet une interprétation qui n'est pas possible avec des essais de 96 h au cours desquels les CL50 sont mesurées à intervalles de 24 h.

Received July 3, 1975
Accepted October 31, 1975

Reçu le 3 juillet 1975
Accepté le 31 octobre 1975

HEXAVALENT chromium, sodium chloride, pentachlorophenol, and Guthion® (azinphos-methyl) have been released into natural waters from various industrial processes, from runoff waters, or from agricultural uses. Some information is available on the acute toxicity of these compounds to fishes, but most of it is for shorter time periods than the tests reported herein and therefore represents acute mortality in terms of individual LC50's, or median survival times at arbitrary times or concentrations, rather than toxicity curves.

[1]Paper No. 9163 Scientific Journal Series, Minnesota Agricultural Experiment Station, St. Paul, Minn., USA.

Printed in Canada (J3896)
Imprimé au Canada (J3896)

Sprague (1969) indicated that toxicity curves were a superior means of describing acute mortality. Brown (1973) also suggested that comparison of relative sensitivities of different species after arbitrary exposure periods is somewhat meaningless and may be misleading. Comparison of mortality by use of toxicity curves, or at least threshold LC50's derived from the curves, would be superior since species differences in LC50's during early exposure periods may be negated or reversed by the time the species has achieved homeostasis with the toxicant. Comparison of toxicity curves can also be more useful in interpretation of acute toxicity since curves having more than one inflection may indicate different modes of toxic action or physiological changes in the fish after exposure. The purpose of the present study was to determine lethal concentrations (LC50's) for the four toxicants with fathead minnows (*Pimephales promelas*) and goldfish (*Carassius auratus*) and to compare the resistance of the two species in these acute exposures by means of toxicity curves representing mortality over the entire test period.

Materials and Methods

Fish Stocks

Fathead minnows were reared in a laboratory hatchery similar to that designed at the National Water Quality Laboratory (U.S. Environmental Protection Agency 1971). The original stock of juvenile fish was obtained from the National Water Quality Laboratory at Duluth, and at approximately 8- to 10-mo intervals additional spawning stock from Duluth was mixed with the hatchery-reared spawners to prevent development of a genetically divergent strain. Stocks of fish tested were spawned within a 1-wk period. The fathead minnows tested in this study were 11 wk old at the start of each test, and mean weights ranged from 0.12 to 0.38 g.

Goldfish were obtained from Ozark Fisheries, Inc., Stoutland, Missouri. During the 2-yr testing period eight shipments were obtained and each stock was tested for resistance to each toxicant. All stocks were treated with 1 mg/liter potassium permanganate for ½ h twice on successive days to remove *Gyrodactylus*. On the third day they were treated with 25 mg/liter tetracycline. After treatment, fish were held for at least 10 days at 21 C in flowing water prior to testing. The goldfish varied in age from 5 mo to 1½ yr and mean weights ranged from 1.37 to 2.70 g.

Toxicity Tests

Toxicity tests of hexavalent chromium and pentachlorophenol were conducted in the same two proportional diluters (Mount and Brungs 1967). Each diluter dispensed seven toxicant concentrations with a dilution factor of 60% and a control. A series of flow splitters permitted duplication of each toxicant concentration and control so that four separate tests could be conducted simultaneously. The test chambers were constructed of glass and G. E. Silicone Seal, measured 50 × 25 × 20 cm, and contained 20 liters. With a flow rate of 105 ml/min, 90% replacement of water occurred in approximately 7 h. The pH was controlled by dispensing sulfuric acid into the head tank with a chemical metering apparatus (Mount and Brungs 1967) and the temperature was controlled by a hot water heat-exchange system in the head tank. Hexavalent chromium was reagent grade potassium dichromate, and pentachlorophenol was technical grade sodium pentachlorophenate. A complete analysis of the well water used (210 mg/liter $CaCO_3$ total hardness) was reported by Adelman and Smith (1972).

Inability to dissolve adequate concentrations of sodium chloride and Guthion® in the proportional diluters necessitated the use of modified static tests. The same number and size test chambers were used as for the toxicants tested under flow-through conditions. Each test chamber contained a 50-W aquarium heater and was aerated continuously.

Preliminary tests indicated that high pH levels in the aerated laboratory water resulted in sublethal accumulations of unionized ammonia. In order to maintain a lower pH and keep the ammonia in a non toxic ionized form, a soft water was used in these tests. This water was prepared by diluting laboratory water with 80% deionized water and buffering with 272 mg/liter monobasic potassium phosphate and 25 mg/liter sodium hydroxide. A fresh preparation of this water was added to each chamber at the start of each test, and 88% of the water and toxicant was changed every 2 or 3 days during the test. Chemical analysis indicated that there was no reduction of either sodium chloride or Guthion® under these conditions for up to 4 days. Reagent grade sodium chloride crystals were dissolved directly into each test chamber, and 93% technical grade Guthion® in an acetone carrier was pipetted directly. One control chamber for each species received a volume of acetone equivalent to that of the highest Guthion® concentration (1750 ppm); no more than 10% mortality was ever observed in this chamber, or in a control chamber without acetone.

From 68 to 72 h prior to the introduction of toxicant, fish were sorted in a stratified random manner into the two sets of test chambers with 10 fish in each. After acclimation to the test chamber, test water, and temperature, the toxicant was immediately brought to the desired concentration by pipetting from a stock solution for Guthion®, sodium pentachlorophenate, and potassium dichromate, and direct dissolution for sodium chloride. In the series of eight tests an error in calculation resulted in about 35% of the desired hexavalent chromium concentration initially, and desired concentrations were not attained for 3–4 h. In three additional tests with each species the desired concentration was immediately attained and results compared to the previous series. Goldfish were acclimated for at least 10 days at 21 C

and then for 3 days at the 25 C test temperature. Fathead minnows were reared at a constant 25 C. Photoperiod during the tests consisted of 12 h of light and 12 h of dark. Dissolved oxygen, pH, temperature, and total alkalinity were monitored routinely during each test. Mean oxygen concentrations in all tests ranged from 5.00 to 7.58 mg/liter and mean temperatures from 23.6 to 26.2 C. In tests conducted in soft water, mean pH meter readings ranged from 6.95 to 7.41, and total alkalinities from 73 to 100 mg/liter $CaCO_3$. In tests with hard water the pH meter readings ranged from 7.47 to 7.86, and alkalinities from 200 to 230 mg/liter $CaCO_3$.

Tests were conducted for 11 days, or until no mortality occurred for 2 days, whichever came first. Two days with no deaths was used as the criterion for achieving a threshold LC50. This threshold LC50 indicates the concentration at which 50% of the fish have achieved apparent homeostasis with the toxicant and no additional acute mortality is likely to occur. Mortality was recorded continuously during the first 8–12 h and at 24-h intervals thereafter. The LC50 values were determined graphically (American Public Health Association 1971). Eight series of tests were conducted in duplicate for a total of 16 tests per species per toxicant. Mean LC50's and 95% confidence intervals around the means were calculated from all 16 tests.

Toxicant Analysis

Concentrations of toxicant in each test chamber were analyzed at 2- or 3-day intervals. In addition, composite samples of pentachlorophenol were accumulated twice a day for the last five series of tests and analyzed at the end. A comparative analysis of fresh and stored samples indicated no deterioration of toxicant.

Hexavalent chromium was analyzed colorimetrically using method 211 (II)D, and chloride by mercuric nitrate titration, method 112 B (American Public Health Association 1971) and results were reported as sodium chloride. In the first three series of tests pentachlorophenol was analyzed colorimetrically after addition of Safranin-O and extraction into chloroform (Haskins 1951). In the last five series pentachlorophenol was extracted into benzene, acetylated, and analyzed on a Beckman GC 72-5 gas chromatograph with a 122-cm glass column packed with 5% DC 200 on 80/100 mesh Gas Chrom-Q and a nonradioactive electron capture detector (Rudling 1970). Comparison of the colorimetric and gas chromatographic methods indicated no difference. Guthion® was analyzed with the same gas chromatographic parameters after extraction into benzene.

Results and Discussion

Sodium Chloride

Most mortality from sodium chloride occurred within the first 48 h, after which the toxicity curves paralleled the abscissa (Fig. 1). Goldfish were initially more resistant than fathead minnows but after 48 h became significantly less resistant with a threshold LC50 of 7322 ± 224 mg/liter for goldfish and 7650 ± 234 mg/liter for fathead minnows ($t = 2.159$, $P = 0.02$–0.05).

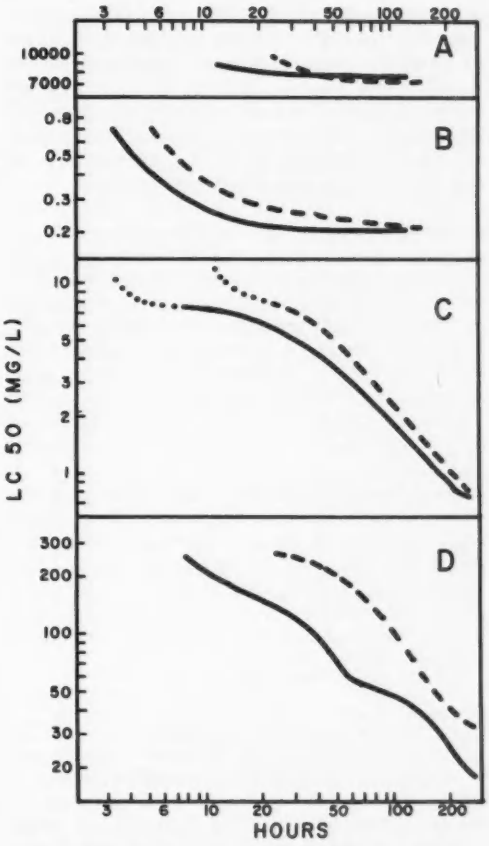

FIG. 1. Toxicity curves of A) sodium chloride, B) pentachlorophenol, C) Guthion,® and D) hexavalent chromium, for goldfish (*Carassius auratus*) (dashed lines) and fathead minnow (*Pimephales promelas* (solid lines). At times of 24 h or longer, curves were visually fitted through mean LC50's from at least 14 tests and at earlier times through mean LC50's from at least eight tests. Hypothesized extensions of the Guthion® curves based on limited data are represented by dots.

Immediately upon introduction of sodium chloride both species were affected even at concentrations that caused no mortality during the tests. For about the first 5 min of exposure there was increased swimming activity, particularly toward the water surface. After this the fish settled into

a pattern of normal activity and food searching near the aquarium bottom. Within 1–2 h prior to death fish began increased respiratory movements at the surface accompanied by occasional bursts of frenzied swimming. Just prior to death swimming ceased and opercular movements slowed considerably. Death was presumed to be due to massive osmoregulatory failure.

Pentachlorophenol

Toxicity curves for pentachlorophenol were similar to those for sodium chloride in that initial mortality was rapid and the curves became parallel to the abscissa by 48 h for fathead minnows and by about 96 h for goldfish (Fig. 1). Again, goldfish were initially more resistant but there was no significant difference in the threshold LC50 of 0.21 ± 0.01 and 0.21 ± 0.02 for fathead minnows and goldfish ($t = 0.117$, $P > 0.5$).

Fish exposed to pentachlorophenol seemed unaffected until a few hours before death. They then exhibited increased swimming activity near the surface, followed by quiescence, then death at the bottom. Webb and Brett (1973) list toxic effects of pentachlorophenol and classify it as a general metabolic stressor, uncoupling oxidative phosphorylation.

Guthion®

The toxicity curves for Guthion® are similar in shape for both species but differ from the curves for sodium chloride and pentachlorophenol as well as typical curves for many other toxicants as reported by Sprague (1969). The curves are nearly parallel to the abscissa at 6–12 h for fathead minnows and at 18–26 h for goldfish (Fig. 1). This result is presumed to be an artifact resulting from concentrations too low to cause measurable mortality sooner than 6 h for fathead minnows and 18 h for goldfish in most tests. In two tests with goldfish where test concentrations were set somewhat higher and early mortality occurred, the mean 8-h LC50 was 17 mg/liter, and the mean 4-h LC50 from two fathead minnow tests under similar conditions was 8.5 mg/liter. As indicated by the dotted line (Fig. 1), it is hypothesized that these curves bend steeply upward at shorter time intervals. The resultant change in slope throughout the curves may indicate different mechanisms of toxic action or at least a period of physiological adjustment before further mortality occurs. The toxic effect of Guthion® and its oxidized metabolite is inhibition of acetylcholinesterase (Chemagro Division Research Staff 1974).

As with sodium chloride and pentachlorophenol, goldfish were initially more resistant, but by the end of the test the 11-day LC50's, 0.76 ± 0.22 mg/liter for fatheads and 0.80 ± 0.15 mg/liter for goldfish, were not significantly different ($t = 0.381$, $P > 0.5$).

Early mortality of fathead minnows was poorly related to toxicant concentration. In a typical test the following percentage mortalities had occurred after 1 h:

Concn (mg/l):	0	0.5	0.9	1.6	2.5	4.8	6.8	10.0
% mortality:	0	20	0	0	20	40	90	40

Upon introduction of the Guthion® fish in all concentrations would appear stressed within 5 min, many lost equilibrium, and some died as indicated by the results above. After initial losses, mortality decreased for up to 24 h and then again increased (Fig. 1). Fish that lost equilibrium would either die almost immediately or would lie on the bottom of the aquarium in this condition for a few days before death occurred. This loss of equilibrium in the environment would be essentially equivalent to death since the individual is immediately vulnerable to predators and is at the mercy of water currents. Therefore, LC50 is not a good predictor of environmental damage. EC50's based on loss of equilibrium would be lower than LC50's at the same time intervals.

Hexavalent Chromium

The toxicity curves for hexavalent chromium are somewhat unusual when compared to typical hyperbolic curves of other toxicants (Fig. 1). The shape of the curve for goldfish is similar to the Guthion® curves and limited data obtained for earlier times suggest that it bends sharply upward at the shorter time intervals. The curve for fatheads indicates an initial period of rapid mortality, followed by a period of reduced mortality. This curve suggests the possibility of two modes of toxic action, one at high and one at lower chromium concentrations. Grindley (1946) reported a similar curve showing the effect of potassium dichromate on rainbow trout. However, this test was conducted at considerably higher concentrations of chromium. In a series of studies on the toxic effect of hexavalent chromium it was found that the primary path of entry was by diffusion through the gills of rainbow trout (*Salmo gairdneri*) (Knoll and Fromm 1960), that no gill pathology occurred but the epithelial cell lining of the intestinal tract was sloughed off in largemouth bass (*Micropterus salmoides*) (Fromm and Schiffman 1958), and that glucose uptake by epithelial cells of the intestinal tract was inhibited (Stokes and Fromm

1965). These authors did not suggest more than one mode of toxic action.

With the other three toxicants the goldfish were initially more resistant but by the end of the test, LC50's were the same for both species (pentachlorophenol and Guthion®) or less for goldfish (sodium chloride). With hexavalent chromium the goldfish were more resistant throughout the entire test. The 11-day LC50 for goldfish, 33 ± 7 mg/liter, was significantly greater than for fathead minnows, 18 ± 2 mg/liter ($t = 4.601$, $P = 0.01$–0.02). Unless these species differ considerably in their resistance to chromium as compared to the other toxicants, it might be expected that after 11 days the chromium toxicity curve for goldfish would bend downward resulting in a curve similar to that for fathead minnows.

Since initial chromium concentrations were gradually increased to the desired concentrations in the previously reported tests, three tests on each species were conducted to compare the difference in LC50's when test concentrations were attained immediately. The toxicity curves for both species were similar in shape to the curves obtained by the first experimental procedure (Fig. 2). The LC50's for fathead minnows were lower at all times, but the LC50's for goldfish were higher after 24 h, than in the first set of experiments. The difference in procedure increased acute mortality of fathead minnows throughout the test period, and the 11-day LC50 by the first procedure, 18 ± 2 mg/liter, was significantly higher than the 11-day LC50 by the second procedure, 12 ± 8 mg/liter ($t = 2.482$, $P = 0.02$–0.05). Toxicity to goldfish using the two procedures was not significantly different ($t = 0.722$, $P > 0.5$).

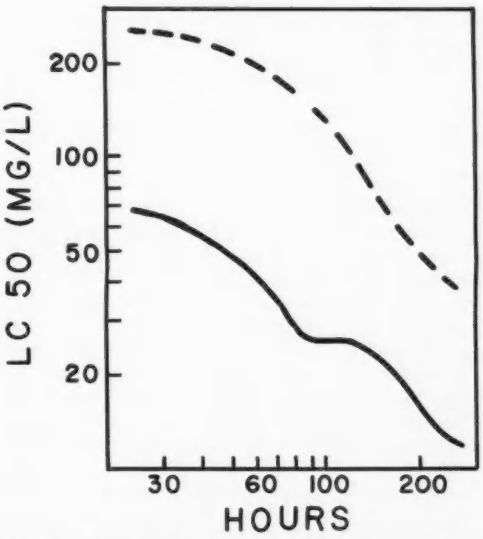

FIG. 2. Toxicity curves of hexavalent chromium for goldfish (dashed line) and fathead minnow (solid line). Curves were visually fitted through mean LC50's from three tests using the second experimental procedure.

The onset of detrimental effects was usually observable from 24 to 48 h before death. Respiratory movements became more rapid and pronounced and fish surfaced frequently. Prior to death respiratory movements slowed, fish lost equilibrium, and they died shortly thereafter. Within 24 h after introduction of even the lowest chromium concentrations tested, the bottom of the goldfish chambers became littered with tapeworms.

The foregoing series of experiments demonstrate that the examination of toxicity curves in assessing acute mortality of toxicants allows comparison between species and toxicants that might not be evident from typical 96-h tests where LC50's are computed only at 24-h intervals.

Acknowledgments

The project was supported in part by a grant from the U.S. Environmental Protection Agency under grant number 800940. We thank R. Ruesink for assistance in conducting experiments.

ADELMAN, I. R., AND L. L. SMITH JR. 1972. Toxicity of hydrogen sulfide to goldfish (*Carassius auratus*) as influenced by temperature, oxygen, and bioassay techniques. J. Fish. Res. Board Can. 29: 1309–1317.

AMERICAN PUBLIC HEALTH ASSOCIATION, AMERICAN WATER WORKS ASSOCIATION, AND WATER POLLUTION CONTROL FEDERATION. 1971. Standard methods for the examination of water and wastewater. 13th ed. New York, N.Y. 874 p.

BROWN, V. M. 1973. Concepts and outlook in testing the toxicity of substances to fish, p. 73–96. *In* G. E. Glass [ed.] Bioassay techniques and environmental chemistry. Ann Arbor Sci. Publ. Inc., Ann Arbor, Mich.

CHEMAGRO DIVISION RESEARCH STAFF. 1974. Guthion® (azinphosmethyl): organophosphorus insecticide. Residue Rev. 51: 123–180.

FROMM, P. O., AND R. H. SCHIFFMAN. 1958. Toxic action of hexavalent chromium on largemouth bass. J. Wildl. Manage. 22: 40–44.

GRINDLEY, J. 1946. Toxicity to rainbow trout and minnows of some substances known to be present in waste waters discharged to rivers. Ann. Appl. Biol. 33: 103–112.

HASKINS, W. T. 1951. Colorimetric determination of microgram quantities of sodium and copper pentachlorophenates. Anal. Chem. 23: 1672–1674.

KNOLL, J., AND P. O. FROMM. 1960. Accumulation and elimination of hexavalent chromium in rainbow trout. Physiol. Zool. 33: 1–8.

MOUNT, D. I., AND W. A. BRUNGS. 1967. A simplified dosing apparatus for fish toxicology studies. Water Res. 1: 21–29.

RUDLING, L. 1970. Determination of pentachlorophenol in organic tissues and water. Water Res. 4: 533–537.

SPRAGUE, J. B. 1969. Measurement of pollutant toxicity to fish. I. Bioassay methods for acute toxicity. Water Res. 3: 793–821.

STOKES, R. M., AND P. O. FROMM. 1965. Effects of chromate on glucose transport by the gut of rainbow trout. Physiol. Zool. 38: 202–205.

U.S. ENVIRONMENTAL PROTECTION AGENCY. 1971. Tentative plans for the design and operation of a fathead minnow stock culture unit. Natl. Water Quality Lab. Duluth, Minn. 8 p.

WEBB, P. W., AND J. R. BRETT. 1973. Effects of sublethal concentrations of sodium pentachlorophenate on growth rate, food conversion efficiency, and swimming performance in underyearling sockeye salmon (*Oncorhynchus nerka*). J. Fish. Res. Board Can. 30: 499–507.

Fathead Minnows (*Pimephales promelas*) and Goldfish (*Carassius auratus*) as Standard Fish in Bioassays and Their Reaction to Potential Reference Toxicants[1]

IRA R. ADELMAN AND LLOYD L. SMITH JR.

Department of Entomology, Fisheries, and Wildlife, University of Minnesota, St. Paul, Minn. 55108, USA

ADELMAN, I. R., AND L. L. SMITH JR. 1976. Fathead minnows (*Pimephales promelas*) and goldfish (*Carassius auratus*) as standard fish in bioassays and their reaction to potential reference toxicants. J. Fish. Res. Board Can. 33: 209–214.

Fathead minnows (*Pimephales promelas*) and goldfish (*Carassius auratus*) were compared for their suitability as standard bioassay fish. Both species showed the same variability of bioassay results when tested with four toxicants. Fathead minnows are recommended on the basis of their small size and on their capability for use in complete life cycle tests.

On the basis of minimum variability of bioassay results, sodium chloride was superior for use as a reference toxicant. Both sodium chloride and pentachlorophenol seemed capable of detecting abnormal fish. On the basis of seven listed criteria either sodium chloride or pentachlorophenol would be acceptable as a reference toxicant.

ADELMAN, I. R., AND L. L. SMITH JR. 1976. Fathead minnows (*Pimephales promelas*) and goldfish (*Carassius auratus*) as standard fish in bioassays and their reaction to potential reference toxicants. J. Fish. Res. Board Can. 33: 209–214.

Nous avons comparé des têtes-de-boule (*Pimephales promelas*) et des poissons dorés (*Carassius auratus*) comme sujets d'essais biologiques conventionnels. Les deux espèces montrent la même variabilité dans les résultats d'analyse lorsque exposées à quatre toxiques. Nous recommandons l'emploi de têtes-de-boule à cause de leur taille plus petite et parce qu'ils peuvent être utilisés dans des essais impliquant un cycle biologique complet.

Sur une base de variabilité minimale des résultats d'analyses biologiques, le chlorure de sodium est supérieur comme toxique-type. Le chlorure de sodium et le pentachlorophénol sont tous deux capables de détecter les poissons anormaux. D'après sept critères énumérés, le chlorure de sodium ou le pentachlorophénol seraient l'un ou l'autre acceptables comme toxique-type.

Received July 3, 1975
Accepted October 31, 1975

Reçu le 3 juillet 1975
Accepté le 31 octobre 1975

MANY authors have mentioned the desirability of using a standard fish species as a bioassay animal to allow for reproducibility of test results (Marking 1966; Lennon 1967; Cairns 1969; Sprague 1970). Since resistance to a toxicant may vary with species, strain, previous history, age, size, health, and handling procedures, the first step in achieving reproducibility within or between laboratories would be development of standard bioassay procedures and a standard bioassay fish.

The more important criteria for selection of any strain used as a standard fish for bioassay are: 1) relatively constant response to a broad range of toxicants when tested under similar conditions; 2) availability in large quantities with close quality control; 3) easily handled for bioassay purposes; 4) easily transported; 5) continuous availability of the desired size; and 6) capable of successful completion of a life cycle in 1 yr or less.

One objective of the present study was primarily related to the first criterion. If a standard strain is used to make comparisons within or between laboratories, that strain must not show high variability in response when tested under standardized procedures at different times or locations. To assess variability, acute bioassays were conducted over a 2-yr period with two species frequently suggested as potential standard fish and four toxicants with presumably different modes of toxic action. Goldfish (*Carassius auratus*) were chosen because of their availability

[1]Paper No. 9163 Scientific Journal Series, Minnesota Agricultural Experiment Station, St. Paul, Minn., USA.

Printed in Canada (J3897)
Imprimé au Canada (J3897)

in large quantities from a single commercial source, Ozark Fisheries, Inc., Stoutland, Missouri, and because of their proposed use in a standard bioassay procedure for industries in the Ohio River valley (ORSANCO 1974). Fathead minnows (*Pimephales promelas*) were selected because of successful use in many bioassays (Martin 1973). The U.S. Environmental Protection Agency (1971) developed a small-scale hatchery design and therefore the technology for development of a commercial source is available.

Sodium chloride, pentachlorophenol, hexavalent chromium, and Guthion® were selected on the basis of their presumed different modes of toxic action (Adelman et al. 1976) in order to expose fish to a variety of compounds. The first three were also selected for their potential as a reference toxicant. Marking (1966) and Davis and Hoos (1975) have discussed the need for a reference toxicant to determine the condition of fish at the time of testing. In theory, a reference toxicant bioassay under standardized test conditions would be conducted just prior to, or simultaneously with, a bioassay of the toxicant or effluent under consideration. If results from the reference toxicant bioassay deviated considerably from previously accumulated data on this toxicant, the fish stock would be considered abnormal and results of any bioassays with it would be questionable.

As with the standard fish strain, a reference toxicant should meet certain criteria to be useful. The more important criteria are: 1) minimum variability in response of normal fish; 2) rapid detection of abnormal fish by a deviant response; 3) rapid lethal action; 4) simple analytical technique; 5) usable in static and flow-through bioassays; and 6) general ease of laboratory handling. A second objective of this study was to determine how well the test materials met these criteria.

Experimental Design

Flow-through bioassays were conducted with pentachlorophenol and hexavalent chromium and static bioassays were conducted with sodium chloride and Guthion®. A complete description of the materials and methods is included in Adelman et al. (1976). Eight tests were conducted in duplicate with each species and each toxicant over a 2-yr period to determine the variability of bioassay results. Fathead minnows from our laboratory hatchery were tested when 11 wk old and eight stocks of goldfish were obtained from the commercial source and tested during this period. The experimental design permitted a determination of the coefficient of variation (CV) for the 24-h, 96-h, and threshold or 11-day LC50's for each toxicant with each species. Two days with no deaths was used as the criterion for achieving a threshold LC50. Since each individual bioassay was conducted in duplicate, multiway analyses of variance of the LC50's were used to determine significant differences between different stocks of fish and between the two sets of bioassay aquaria in which the duplicates were conducted. To estimate the probability of an uncontrolled variable affecting the LC50's with different fish stocks, a modification of the standard multiway analysis of variance was used where error due to the slope of individual treatments against their deviation from the mean response was partitioned (Mandel 1961).

Since eight analyses were performed at each time interval, a rigid per comparison error rate of 0.0064 was computed [$\alpha = 1 - (1 - p)^{1/n}$] for rejection of the null hypothesis to reduce the possibility of making at least one Type I error by chance. This per comparison error rate of 0.0064 was equivalent to a per experiment error rate of 0.05 with the experiment consisting of eight (n) analyses of variance at each time interval (two species, four toxicants).

In order to test the ability of the toxicant to detect a previously unhealthy and stressed stock of fish by showing abnormal LC50's, a stock of goldfish that arrived in extremely poor condition, heavily infested with skin flukes and probably a bacterial disease, was tested with each toxicant. Prior to bioassay daily mortality was high for over a month and during that period numerous treatments with potassium permanganate, tetracycline, or neomycin were administered. After about a 50% loss, the mortality ceased and the fish were tested in duplicate with each toxicant.

Results and Discussion

Variability of Test Species

Adelman et al. (1976) discussed the mortality of fish due to the four toxicants in terms of toxicity curves depicting death rates during the entire test. Standard bioassays by industrial or research laboratories will probably continue to report results as LC50's at fixed times, most likely 24 h as with the ORSANCO (1974) bioassay, or 96 h as has become almost standard practice in many countries. Reporting of threshold LC50's has become common where these values are attained in a relatively short time. Therefore, the comparison of variability described here is in terms of 24- and 96-h LC50's for all toxicants, threshold LC50's for sodium chloride and pentachlorophenol, and 11-day LC50's for hexavalent chromium and Guthion® with which threshold values were not attained by termination of the bioassay.

Sodium chloride LC50 values were the least variable of the four toxicants at all times, with essentially no difference in coefficient of variation between fathead minnows and goldfish (Table 1). Pentachlorophenol ranked second although

TABLE 1. Mean LC50's (milligrams/liter) and coefficients of variation at different times.

	Time					
	24 h		96 h		Terminal[a]	
Toxicant	LC50	CV	LC50	CV	LC50	CV
			Fathead minnows			
NaCl	7910	8	7650	6	7650	6
PCP	0.22	19	0.21	12	0.21	12
Cr^{+6}	140	20	48	22	18	21
Guthion®	5.94	58	1.90	39	0.76	52
			Goldfish			
NaCl	9952	7	7341	6	7322	6
PCP	0.27	23	0.22	17	0.21	16
Cr^{+6}	261+	—[b]	120	12	33	38
Guthion®	7.78	24	2.37	29	0.80	35

[a]Threshold LC50 for NaCl and PCP, 11-day LC50 for Cr^{+6} and Guthion®.
[b]24-h LC50 not obtained in all tests due to slow mortality.

with this toxicant goldfish were slightly more variable than fatheads. Hexavalent chromium and Guthion® ranked third and fourth, respectively, although missing data and some variation at different times make this ranking somewhat less definitive. With sodium chloride and pentachlorophenol there was little difference between variability of 96-h and threshold LC50's, but variability at 24 h was greater than at the other times. With hexavalent chromium there was essentially no difference between variability of 24-h, 96-h, and 11-day LC50's with fathead minnows, but with goldfish the variability of the 96-h LC50 was considerably less than at 11 days; because initial mortality was slow, too few 24-h LC50's were determined for computation of a reliable coefficient. The fathead minnows had minimum variability to Guthion® at 96 h and similar variability at 1 and 11 days, whereas the goldfish showed increasing variability at 1, 4, and 11 days. In general, the 96-h measurement was the least variable, but where threshold values were attained, they showed similar variability.

Neither fish species showed consistent superiority in minimal variability. Both were the same for sodium chloride; the fathead minnows were slightly less variable with pentachlorophenol and considerably more variable with Guthion®. With chromium the goldfish were less variable at 96 h and more variable at 11 days; no comparison was available at 24 h.

The analyses of variance indicated only one instance of a significant difference between the duplicate bioassay apparatus used for testing each stock. That difference occurred with goldfish at 96 h testing hexavalent chromium. Since there was also a significant difference in slope, it appeared that some independent variable was responsible for the difference between results from the two apparatus. Correlation coefficients were computed for the LC50's and all quantifiable independent variables, which included weight, length, condition factor, age of fish, time of prebioassay holding, dissolved oxygen concentration, pH, and temperature. Only temperature correlated ($r = -0.69$). An analysis of covariance with temperature as the covariate was computed and the results from the two bioassay apparatus were still significantly different, indicating that temperature was not the cause of the difference. Since slope was not significantly different in any other comparison, there was no indication of an independent variable affecting the LC50's.

REFERENCE TOXICANT

The same data used to evaluate the variability of the two fish species also indicate the variability of the toxicants. Sodium chloride bioassays were considerably less variable at all times (Table 1). Therefore, this compound best meets the criterion of minimum variability in response of the fish to a reference toxicant. Pentachlorophenol ranked second in variability, and although the CV was about 2–3 times greater than for sodium chloride, it is still acceptable as a reference toxicant. The CV's for chromium and Guthion® were considerably higher and varied so much between species that neither is suitable as a reference toxicant on the basis of this criterion.

The results of the bioassays can be used only indirectly to assess whether the toxicant would detect abnormal fish by their having a deviant response. If stocks of fish, particularly goldfish,

TABLE 2. Comparison of LC50's (milligrams/liter) from unhealthy goldfish (*Carassius auratus*) stock with mean LC50's from all tests with "normal" goldfish.

		NaCl	PCP	Cr^{+6}	Guthion®
		24-h LC50			
"Normal"	Mean	9952	0.27	—	7.78
	Range	8350–11050	0.18–0.37	—	5.34–11.20
Unhealthy	Test 1	9270	0.38	—	7.35
	Test 2	10270	0.44	—	6.25
		96-h LC50			
"Normal"	Mean	7341	0.22	120	2.37
	Range	6800–8050	0.17–0.30	90–135	1.35–3.86
Unhealthy	Test 1	6170	0.24	93	<0.18
	Test 2	6180	0.30	106	0.17
		Terminal LC50[a]			
"Normal"	Mean	7322	0.21	33	0.80
	Range	6800–8050	0.15–0.28	15–59	0.19–1.22
Unhealthy	Test 1	6170	0.19	37	<0.18
	Test 2	6180	0.25	56	<0.17

[a]Threshold LC50 for NaCl and PCP, 11-day LC50 for Cr^{+6} and Guthion®.

differed during the 2-yr period of testing, the experimental design would permit detection of these differences in response to the toxicants by the multiway analysis of variance. Only the sodium chloride bioassays consistently revealed a significant difference between the eight stocks of fish tested with both the 96-h and threshold LC50's different for both species. Three other indications of significant differences between fish stocks, goldfish with pentachlorophenol at 24 h, and fathead minnows with chromium at 96 h and Guthion® at 24 h, were not consistent between species or other test durations. Since the same stock of goldfish was tested with each toxicant, significant differences might be expected with all toxicants. However, bioassay results with sodium chloride were considerably less variable (Table 1), and thus significant differences between stocks tested with the other toxicants were either masked by the greater overall variability or did not occur. Therefore, sodium chloride appears to be the most sensitive indicator of differences between fish stocks. Whether or not these differences are due to previous history of the stock, fish conditions at the time of testing, or some uncontrolled variable cannot be evaluated from these data.

In the one direct attempt to determine if the toxicants would detect unhealthy goldfish, it was hypothesized that these fish would either be more resistant to the toxicants if the weaker individuals had been eliminated from the population, less resistant if the total stress from the diseases and treatments had increased their sensitivity, or equally resistant if the two factors balanced out. With the unhealthy fish the equivalent 96-h and threshold LC50's of sodium chloride were considerably lower than the means from all bioassays with the presumed healthy fish and well outside the range of all of these tests (Table 2). However, the 24-h LC50's were well within the range of other tests. These results correspond to the analyses of variance of the 16 regular bioassays where there were significant differences in 96-h and threshold LC50's but no difference at 24 h. The reverse trend occurred with pentachlorophenol; threshold and 96-h LC50's with the unhealthy fish were within the range of the normal fish, but the 24-h LC50's were greater and outside the range for normal fish (Table 2). These results correspond with the analyses of variance for pentachlorophenol where differences in stocks of goldfish were detected at 24 h but not at the other 2 times. The only other instances where the LC50's for the unhealthy fish were outside the range for normal fish were the 96-h and 11-day values for Guthion® (Table 2). The analyses of variance did not detect stock differences with Guthion® at these times, but the great overall variability of Guthion® probably masked any possible differences.

A reference toxicant should be suitable for use in either flow-through or static systems depending on the needs of the laboratory. With flow-through systems currently in use it is impractical to use sodium chloride because the quantity of salt required is too great. Pentachlorophenol can be used for tests in either system. When the same

TABLE 3. Comparison of four toxicants with regard to their use as a reference toxicant.[a]

	NaCl	PCP	Cr^{+6}	Guthion®
Consistency of fish response	1	2	3	4
Detection of abnormal fish	2	2	4	3
Rapid attainment of threshold LC50	1	1	4	4
Use in static bioassay	2	2	2	2
Use in flow-through bioassay	4	1	1	3
Ease of chemical analysis	1	3	1	4
General ease in handling	2	2	3	4

[a]1, very good; 2, good; 3, fair; 4, poor.

stock of goldfish was tested simultaneously in duplicate static bioassays and duplicate flow-through systems, the threshold LC50's were 1.5–2 times greater in the static tests. The cause of this difference was not determined. It was not due to deterioration or loss of toxicant in the static since concentrations were monitored daily and no change occurred. No static bioassays were attempted with hexavalent chromium but others have conducted apparently successful static tests (Trama and Benoit 1960). Although static Guthion® tests were performed, flow-through bioassays are possible as was demonstrated in a chronic test conducted in our laboratory. The major difficulty with a flow-through acute bioassay was getting the Guthion® into solution at the high concentrations needed.

Table 3 summarizes the ability of the four toxicants to meet seven desired characteristics of a reference toxicant. The first five criteria (top to bottom) have been discussed in depth in this paper and by Adelman et al. (1976). Ease of chemical analysis is an important consideration for research laboratories, but industrial laboratories will probably use calculated concentrations without chemical analysis. The subjective judgment on ease of handling is based on use of the chemical in a laboratory including such factors as equipment cleaning and administration of the material, and on considerations of degradation of waste material in the environment and toxicity to humans (including carcinogenicity).

CONCLUSIONS

On the basis of minimum variability in results of acute bioassays neither the goldfish nor the fathead minnow was superior and variability was more dependent on the toxicant than on the species. With the toxicants for which a threshold LC50 was attained rapidly, sodium chloride and pentachlorophenol, variability was relatively small, but with Guthion® and hexavalent chromium, where a threshold LC50 was not attained by 11 days, variability was considerably greater. Thus the decision on selection of a standard fish between these two species must be based on other criteria. Both fish are easily handled for bioassay purposes; however, smaller test containers can be used for the juvenile fathead minnows. Both species should be easily transportable since this depends largely on low oxygen tolerance. The fathead minnow has been used successfully in chronic studies since sexual maturity can be achieved in about 5 mo. We have not been able to raise goldfish from an egg to spawning adult in our laboratory and are not aware of anyone having done so under laboratory conditions. On the basis of these biological considerations, the fathead minnow is recommended as the better of the two species for a standard bioassay fish. Since the goldfish is available from a large commercial source it could be used at present; however, regulating agencies could promote the development of a source for fathead minnows.

On the basis of minimum variability and ability to detect abnormal fish sodium chloride best met the requirements for a reference toxicant. Although pentachlorophenol can be used, careful consideration should be given to pH of the test water since toxicity is greatly influenced by pH (Crandall and Goodnight 1959). This necessity might complicate industrial bioassays.

Use of any reference toxicant will require previous standardization by many bioassays in order to establish a baseline with which comparisons can be made. In establishing this baseline, complete information on the fish stocks will be required to eliminate stressed fish from consideration. Since even presumed healthy fish vary, rejection of a bioassay stock should be considered only if it falls outside of the range of baseline tests. Considering normal variability, a more rigid criterion based on standard deviations would be too restrictive and result in rejection of many stocks of fish.

Acknowledgments

This project was supported in part by a grant from the U.S. Environmental Protection Agency under grant number 800940. We thank personnel at the National Water Quality Laboratory, Newtown, for suggestions on selection of species and toxicants.

ADELMAN, I. R., L. L. SMITH, JR., AND G. D. SIESENNOP. 1976. Acute lethal effects of sodium chloride, pentachlorophenol, Guthion®, and hexavalent chromium on fathead minnows (*Pimephales promelas*) and goldfish (*Carassius auratus*). J. Fish. Res. Board Can. 33: 203–208.

CAIRNS, J. JR. 1969. Fish bioassays — reproducibility and rating. Rev. Biol. (Lisbon) 7: 7–12.

CRANDALL, C. A., AND C. J. GOODNIGHT. 1959. The effect of various factors on the toxicity of sodium pentachlorophenate to fish. Limnol. Oceanogr. 4: 53–56.

DAVIS, J. C., AND R. A. W. HOOS. 1975. Use of sodium pentachlorophenate and dehydroabietic acid as reference toxicants for salmonid bioassays. J. Fish. Res. Board Can. 32: 411–416.

LENNON, R. E. 1967. Selected strains of fish as bioassay animals. Prog. Fish Cult. 29: 129–132.

MANDEL, J. 1961. Non-additivity in two-way analysis of variance. J. Am. Stat. Assoc. 56: 878–888.

MARKING, L. L. 1966. Evaluation of *p,p'*-DDT as a reference toxicant in bioassays. U.S. Bur. Sport Fish. Wildl. Resour. Publ. 14: 10 p.

MARTIN, D. M. 1973. Freshwater laboratory bioassays — a tool in environmental decisions. Contrib. Dep. Limnol., Acad. Nat. Sci., Philadelphia, Pa. 3: 51 p.

ORSANCO Biological Water Quality Committee. 1974. ORSANCO 24-hour bioassay. Ohio River Valley Water Sanit. Comm. Cincinnati, Ohio. 21 p.

SPRAGUE, J. B. 1970. Measurement of pollutant toxicity to fish. II. Utilizing and applying bioassay results. Wat. Res. 4: 3–32.

TRAMA, F. B., AND R. J. BENOIT. 1960. Toxicity of hexavalent chromium to bluegills. J. Water Pollut. Control Fed. 32: 868–877.

U.S. Environmental Protection Agency. 1971. Tentative plans for the design and operation of a fathead minnow stock culture unit. Natl. Water Quality Lab., Duluth, Minn. 8 p.

Effects of Antibacterial Agents on Nitrification in an Aquatic Recirculating System

M. T. COLLINS, J. B. GRATZEK, D. L. DAWE, AND T. G. NEMETZ

Department of Medical Microbiology, College of Veterinary Medicine, University of Georgia, Athens, Ga. 30602, USA

COLLINS, M. T., J. B. GRATZEK, D. L. DAWE, AND T. G. NEMETZ. 1976. Effects of antibacterial agents on nitrification in an aquatic recirculating system. J. Fish. Res. Board Can. 33: 215–218.

Treatment of recirculating systems with a single dose of erythromycin (50 mg/liter) resulted in nitrate reduction and stopped nitrification for 14 days as evidenced by changes in pH and ammonia, nitrite and nitrate concentrations. Treatment of systems with 2-chloro-6-(trichloromethyl) pyridine, a known nitrification inhibitor, inhibited nitrification similarly. Treatment with chloramphenicol (50 mg/liter), oxytetracycline (50 mg/liter), sulfamerazine (50 mg/liter), or nifurpirinol (1 mg/liter) had no effect on nitrification.

COLLINS, M. T., J. B. GRATZEK, D. L. DAWE, AND T. G. NEMETZ. 1976. Effects of antibacterial agents on nitrification in an aquatic recirculating system. J. Fish. Res. Board Can. 33: 215–218.

Le traitement des systèmes de recirculation d'eau avec une dose unique d'érythromycine (50 mg/litre) cause une réduction des nitrates et un arrêt de la nitrification pendant 14 jours, comme le démontrent des changements dans le pH et l'ammoniac, et dans les teneurs en nitrites et nitrates. Le traitement de ces systèmes avec de la 2-chloro-6-(trichlorométhyl) pyridine, un inhibiteur connu de nitrification, entraîne également une inhibition de la nitrification. Le traitement avec du chloramphénicol (50 mg/litre), de l'oxytétracycline (50 mg/litre), de la sulfamérazine (50 mg/litre) ou du nifurpirinol (1 mg/litre) est sans effet sur la nitrification.

Received July 26, 1975
Accepted November 12, 1975

Reçu le 26 juillet 1975
Accepté le 12 novembre 1975

ANTIBACTERIAL agents that have found wide usage in fish culture in North America are: sulfamerazine, sulfamethazine, sulfisoxazole, oxytetracycline, chloramphenicol, erythromycin, furazolidone, and nifurpirinol (adapted from Herman 1970). Administration of most of these agents in feed is the most practical method of treating systemic bacterial diseases of fish. Although antibacterial agents may be administered in medicated feed, a certain amount of the agent will leach into the water (Fribourgh 1969). In many instances, antibacterials are added directly to water to treat external bacterial infections, such as myxobacteriosis, or to reduce the load of bacteria in order to prevent bacterial infections (Snieszko and Axelrod 1971).

Whether antibacterial agents enter the water by design or as a consequence of leaching from medicated feed, the question arises as to the effect of these agents on nitrifying bacteria in a recirculating system. Collins et al. (1975a) studied the effects of seven common fish parasiticides on nitrification and found that six of the seven could safely be used in recirculating systems without impeding the nitrification process; only methylene blue (5 mg/liter) was demonstrated to seriously inhibit nitrification. The present study extends the work on recirculating systems to evaluate the effect of six antibacterial agents on the nitrification process. Concentrations of antibacterials chosen for study were based on dosages recommended for use in medicated feed, concentrations recommended for use in water, and concentrations achieved by commercial antibacterial products (Amend 1972, Amlacher 1970; Trust 1972).

Materials and Methods

Twenty-six recirculating systems, similar to those described by Collins et al. (1975a, b) were used. The filter matrix was a mixture of 500 cm^3 of no. 4 quartz gravel and 500 cm^3 of crushed oyster shell. The gravel previously had been in a conditioned recirculating system and carried a complete complement of nitrifying bacteria on its surface. Oyster shell functioned as a buffer. Aquaria were filled with dechlorinated tap water (pH 7.2, hardness 30 ppm as $CaCO_3$). Water was added to replace only that lost by evaporation and sampling. Each aquarium was stocked with 20 channel catfish fingerlings (*Ictalurus*

Printed in Canada (J3922)
Imprimé au Canada (J3922)

TABLE 1. Mean values ($n = 52$) for water quality parameters measured after treatment of recirculating systems.

Treatment	Temp (*C*)	Dissolved oxygen (*mg/liter*)	pH	Total ammonia–nitrogen (*mg/liter*)	Un-ionized ammonia–nitrogen (*mg/liter*)	Nitrite–nitrogen (*mg/liter*)	Nitrate–nitrogen (*mg/liter*)
Control	25.5	6.78	7.59	0.12	0.003	0.06	40.02
Chloramphenicol	25.8	6.80	7.54	0.09	0.002	0.05	46.42
Erythromycin	24.4	7.07	8.14[a]	10.70[a]	1.162[a]	3.18[a]	6.99[a]
Nifurpirinol	25.4	6.77	7.61	0.09	0.002	0.06	40.96
Oxytetracycline	25.3	6.83	7.58	0.10	0.002	0.06	39.23
Sulfamerazine	25.4	7.17	7.60	0.11	0.003	0.05	39.92
2-chloro-6 (trichloromethyl) pyridine	24.7	6.84	7.93[a]	13.61[a]	0.862[a]	0.62	20.53[a]

[a] $P < 0.01$. *P* values based on Dunnett's *t*-test represent significance of difference between control and treated systems.

punctatus), average weight 16.3 g. A commercial fish diet was offered daily at the rate of 1.5% of total body weight.

The recirculating systems were divided into six groups of four aquaria each, one control and five antibacterial treatment groups. Two additional aquaria were treated with 2-chloro-6-(trichloromethyl) pyridine (CTCMP), a known nitrification inhibitor, serving as a positive control. Treatments were administered once by addition directly to the water at the following dosages: chloramphenicol (Chloromycetin® sodium succinate, injectable form, Parke-Davis, Detroit, Mich.); oxytetracycline (oxytetracycline hydrochloride powder, potency 90.5 mcg/mg marketed as Terramycin®, Charles Pfizer Co., New York, N.Y.); sulfamerazine (Sulfamerazine®, Merck, Sharpe and Dohme, Philadelphia, Pa.); erythromycin (Ilosone®, lauryl sulfate salt of the propionyl ester of erythromycin, Eli Lilly and Co., Inc., Indianapolis, Ind.) — all 50 mg/liter; nifurpirinol (Furanase®, Abbott Laboratories, N. Chicago, Ill.) 1 mg/liter; CTCMP (N-SERVE®, Dow Chemical Co., USA) 2 mg/liter. All recirculating systems were operated for 14 days prior to treatment to allow water quality to stabilize and monitored for 26 days after treatment to detect chemical changes in the water.

Water samples (200 ml) were collected directly in glass bottles from the center of each aquarium on alternate days for the duration of the experiment and analyzed immediately after collection. Water temperature, dissolved oxygen, pH, total ammonia–nitrogen, nitrite–nitrogen and nitrate–nitrogen were measured electrometrically and un-ionized ammonia–nitrogen was calculated as described by Collins et al. (1975a, b).

The mean was calculated for each chemical parameter on each day for each treatment group, and a one-way analysis of variance was calculated for each parameter after treatment of the recirculating systems. The mean values thus obtained in the analysis of variance were compared using Dunnett's *t*-test. In this test each treatment mean is compared to the mean of the control.

Results and Discussion

On day 0, prior to treatment, physical and chemical parameters in all 26 systems were not significantly different. Water quality in the recirculating systems (means ± SD, $n = 26$) prior to treatment was:

Temperature (*C*)	25.3	±	0.6
Dissolved O_2 (*mg/liter*)	6.69	±	0.35
pH	7.80	±	0.04
Total NH_4–N (*mg/liter*)	0.10	±	0.01
Un-ionized NH_3–N (*mg/liter*)	0.004	±	0.001
NO_2–N (*mg/liter*)	0.04	±	0.01
NO_3–N (*mg/liter*)	22.91	±	2.00

Effects of antibacterial agents on the physical and chemical parameters measured over a 26-day period following treatment are summarized in Table 1.

In control systems, nitrification proceeded at a steady rate causing predictable water quality changes. The pH gradually declined from 7.88 on day 0 to 7.59 on day 25 (Fig. 1a). Total ammonia, un-ionized ammonia, and nitrite remained stable (Fig. 1b, c) while nitrate rose steadily at the rate of approximately 1.5 mg/liter NO_3–N reaching 59.89 mg/liter NO_3–N on day 26 (Fig. 1d). No fish mortality occurred in control systems.

Treatment of recirculating systems with erythromycin (50 mg/liter) resulted in water quality changes significantly different from the control. The pH increased to 8.46 on day 10 followed by a gradual decline (Fig. 1a). Total ammonia rose to a peak of 23.19 mg/liter NH_4–N on day 14 and then rapidly decreased (Fig. 1b). Changes in un-ionized ammonia followed the same pattern as total ammonia with the peak concentration being 3.006 mg/liter NH_3–N. Nitrite rose imme-

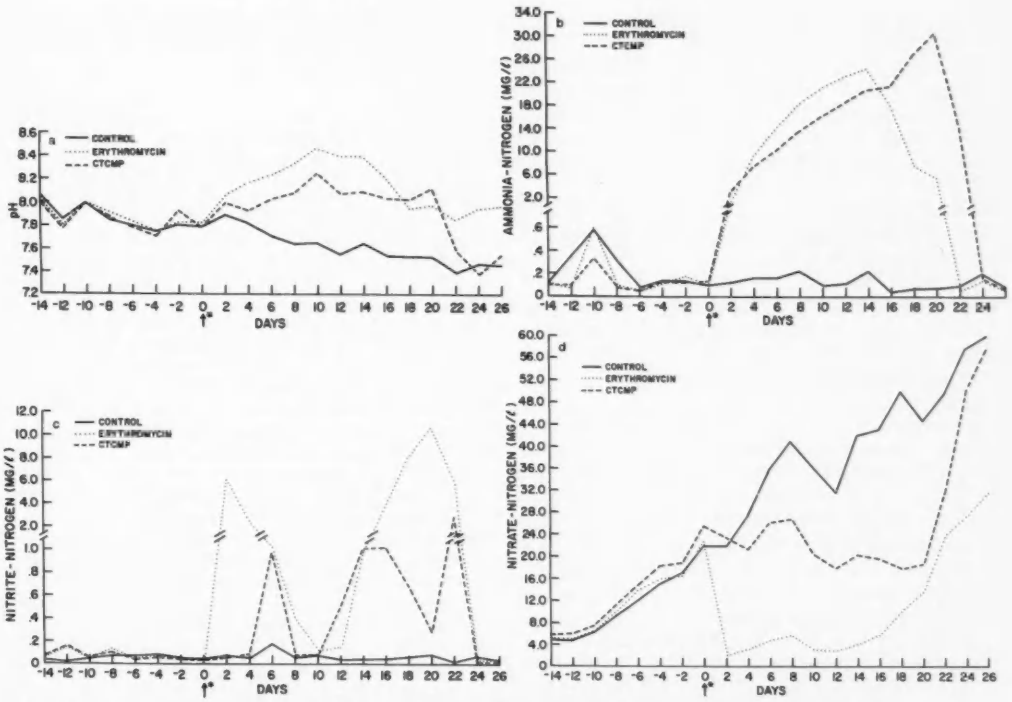

FIG. 1. Changes in a, pH; b, total ammonia concentration; c, nitrite concentration; and d, nitrate concentration in control-, erythromycin-, and CTCMP-treated systems. *First day of treatment.

diately after treatment to 6.16 mg/liter NO_2–N on day 2, gradually declined to 0.12 mg/liter NO_2–N by day 10, rose again to a peak of 10.72 mg/liter NO_2–N on day 20, and rapidly decreased to 0.04 mg/liter NO_2–N on day 24 (Fig. 1c). Nitrate fell immediately after treatment to 2.06 mg/liter NO_3–N on day 2, remained relatively stable until day 16 and then began rising rapidly reaching 31.60 mg/liter NO_3–N on day 26 (Fig. 1d). A cumulative fish mortality of 100% occurred in systems treated with erythromycin. Mortality was highest on days 2, 10, and 20 when ammonia or nitrite concentrations were highest.

Treatment of recirculating systems with erythromycin apparently resulted in conversion of nitrate to nitrite indicating that respiratory reduction of nitrate and possibly denitrification was stimulated for short period of time. Bacteria in the family Enterobacteriaceae and several other common bacteria are capable of respiratory reduction of nitrate. This process occurs to a significant degree only under conditions of reduced oxygen tension. Although a decrease in dissolved oxygen concentration was not measured in the erythromycin-treated systems, a transitory oxygen deficiency could have been responsible for stimulating the conversion of nitrate to nitrite.

In addition to the stimulation of nitrate reduction, nitrification was markedly inhibited in the erythromycin treated systems. Rising pH and ammonia with stable nitrate levels indicate that nitrification had ceased. After a 14-day period of inhibition, nitrification resumed resulting in rapid conversion of ammonia to nitrite and a marked drop in pH. Elevated levels of nitrite lasted 12 days until the nitrite was converted to nitrate. This pattern of water quality changes and heavy fish mortality is similar to that described by Collins et al. (1975b) in an unconditioned recirculating system indicating that both *Nitrosomonas* and *Nitrobacter* bacteria were inhibited or killed by the erythromycin treatment.

N-Serve®, 2-chloro-6-(trichloromethyl) pyridine (CTCMP) is selectively toxic to *Nitrosomonas* sp. bacteria (Campbell and Alleem 1965). Agronomists employ CTCMP to retard the conversion of fertilizer ammonium–nitrogen to nitrate–nitrogen thereby preventing nitrogen loss from soil through leaching or denitrification. CTCMP was

employed in this study as a positive control.

Treatment of recirculating systems with CTCMP (2 mg/liter) resulted in water quality changes similar to those in the erythromycin-treated systems. The pH remained relatively stable until day 20 (Fig. 1a). Total ammonia rose to a peak of 30.58 mg/liter NH_4–N on day 20 and then rapidly declined (Fig. 1b). Unionized ammonia reached a peak of 2.552 mg/liter. Nitrite fluctuated considerably with elevated concentrations of 0.99, 1.16, 1.17, and 2.92 mg/liter NO_2–N on days 6, 14, 16, and 22, respectively (Fig. 1c). Nitrate remained stable until day 20 when it began rising rapidly reaching 57.81 mg/liter on day 26 (Fig. 1d). Cumulative fish mortality was 26% in CTCMP-treated systems.

Changes in pH and ammonia indicate that *Nitrosomonas* bacteria were markedly inhibited in CTCMP-treated systems. The erratic changes in nitrite concentration are difficult to explain, with the exception of the small and transient increase in nitrite between days 20 and 24. This nitrite peak was caused by the recovery of *Nitrosomonas* bacteria which oxidized ammonia to nitrite at a rate that exceeded the capacity of *Nitrobacter* to oxidize the nitrite to nitrate. A comparison of the magnitude of the nitrite peaks in the erythromycin- and CTCMP-treated systems during recovery of nitrification indicates that erythromycin had a much greater affect on *Nitrobacter* than did CTCMP. An examination of changes in nitrate concentration showed that CTCMP treatment virtually stopped nitrification for a period of 20 days.

Treatment with chloramphenicol (50 mg/liter), oxytetracycline (50 mg/liter), sulfamerazine (50 mg/liter), or nifurpirinol (1 mg/liter) did not significantly alter water quality (Table 1). Therefore, these antibacterial agents do not affect nitrification in a recirculating system at the concentrations tested. Coupled with the work by Collins et al. (1975a) on the effects of fish parasiticides on nitrification, it is apparent that most chemical and antibiotic agents can be used safely in recirculating systems. This information should provide added impetus to the development of recirculating systems in fish culture.

Acknowledgments

Funds were provided by the College of Veterinary Medicine in conjunction with the University of Georgia Agricultural Experiment Station, Regional Project S-83, Catfish Breeding, Production, and Marketing. We thank Dr J. M. Bowen, Department of Physiology, for the use of his computer. Donation of oxytetracycline by Pfizer Co. and N-Serve® by Dow Chemical Co. is gratefully acknowledged.

Dr Collins is supported by a National Institutes of Health Fellowship 1 F22 RR 04071-01 from the Animal Resources Branch Division of Research Resources.

AMEND, D. F. 1972. Efficacy, toxicity, and residues of nifurpirinol in salmonids. Bur. Sport Fish. Wildl. Tech. Pap. 62: 13 p.

AMLACHER, E. 1970. Textbook of fish diseases. T.F.H. Publications, Jersey City, N.J. 302 p.

CAMPBELL, N. E. R., AND M. I. H. ALLEEM. 1965. The effect of 2-chloro-6-(trimethyl)pyridine on the chemoautotrophic metabolism of nitrifying bacteria. II. Nitrite oxidation by *Nitrobacter*. Antonie van Leeuwenhock; J. Microbiol. Serol. 31: 137–144.

COLLINS, M. T., J. B. GRATZEK, D. L. DAWE, AND T. G. NEMETZ. 1975a. Effects of common fish parasiticides on nitrification in an aquatic recirculating system. J. Fish. Res. Board Can. 32: 2033–2037.

COLLINS, M. T., J. B. GRATZEK, E. B. SHOTTS JR., D. L. DAWE, L. M. CAMPBELL, AND D. R. SENN. 1975b. Nitrification in an aquatic recirculating system. J. Fish. Res. Board Can. 32: 2025–2031.

FRIBOURGH, J. H., F. P. MEYER, AND J. A. ROBINSON. 1969. Oxytetracycline leaching from medicated fish feeds. Bur. Sport Fish. Wildl. Tech. Pap. 40: 7 p.

HERMAN, R. L. 1970. Prevention and control of fish diseases in hatcheries, p. 3–15. *In* S. F. Snieszko [ed.] A symposium on diseases of fishes and shellfishes. Am. Fish. Soc. Spec. Publ. 5: 526 p.

SNIESZKO, S. F., AND H. R. AXELROD [ed.] 1971. Diseases of fishes. T. F. H. Publications, Jersey City, N.J. 296 p.

TRUST, T. J. 1972. Inadequacy of aquarium antibacterial formulations for the inhibition of potential pathogens of freshwater fish. J. Fish. Res. Board Can. 29: 1425–1430.

Primary Production, Extracellular Release, and Heterotrophy in Two Lakes in the ELA, Northwestern Ontario

C. NALEWAJKO

Scarborough College, University of Toronto, West Hill, Ont. M1C 1A4

AND D. W. SCHINDLER

Department of the Environment, Fisheries and Marine Service, Freshwater Institute, Winnipeg, Man. R3T 2N6

NALEWAJKO, C., AND D. W. SCHINDLER. 1976. Primary production, extracellular release, and heterotrophy in two lakes in the ELA, northwestern Ontario. J. Fish. Res. Board Can. 33: 219–226.

During short-term experiments with phytoplankton, excretion rates of ^{14}C labeled organic substances may change without concomitant changes in photosynthetic rates. Percentage extracellular release (p.e.r.) values generally decreased with time.

In eutrophic Lake 227, p.e.r. after 3-h incubation ranged from about 1 to 4%, depending on light intensity, when phytoplankton biomass was high, but the range was from about 7 to 15% at a time of low biomass. In oligotrophic Lake 239 p.e.r. was about 20%. Mainly large molecules, exceeding 1500 mol wt, were excreted by phytoplankton. A tracer bioassay gave significantly lower estimates of acetate and glucose concentrations than the Michaelis–Menten analysis. Extracellular release rates of dissolved organic compounds by phytoplankton exceeded the total heterotrophic uptake rates of acetate, glucose, and glycollate.

NALEWAJKO, C., AND D. W. SCHINDLER. 1976. Primary production, extracellular release, and heterotrophy in two lakes in the ELA, northwestern Ontario. J. Fish. Res. Board Can. 33: 219–226.

Lors d'expériences à court terme avec le phytoplancton, le taux d'excrétion de substances organiques marquées au ^{14}C peut varier sans qu'il se produise de changements concomitants dans le taux de photosynthèse. Le pourcentage de dégagement extracellullaire (p.d.e.) diminue généralement en fonction du temps.

Dans le lac eutrophe 227, le p.d.e. après incubation de 3 h varie entre 1 et 4% environ, selon l'intensité lumineuse, quand la biomasse de phytoplancton est élevée, mais la gamme est d'environ 7 à 15% quand la biomasse est faible. Dans le lac oligotrophe 239, le p.d.e. est d'environ 20%. Le phytoplancton excrète surtout de grosses molécules, de poids moléculaire dépassant 1500. Une analyse biologique avec traceur donne des estimés significativement plus bas des teneurs en acétate et en glucose que l'analyse de Michaelis–Menten. Les taux de dégagement extracellullaire des composés organiques dissous par le phytoplancton dépasse les taux d'assimilation hétérotrophe totale de l'acétate, du glucose et du glycolate.

Received December 19, 1974
Accepted November 14, 1975

Reçu le 19 décembre 1974
Accepté le 14 novembre 1975

EXTRACELLULAR release in phytoplankton is traditionally measured as percentage extracellular release (p.e.r.) (Watt 1966) and is usually calculated from radioactive dissolved organic carbon ($DO^{14}C$) found in filtrates after incubation of lakewater for several hours with ^{14}C-bicarbonate (Fogg 1971). The implicit assumption is that extracellular release proceeds at a constant rate during the experimental period. However, several investigators have shown that the kinetics of extracellular release in algal cultures may at times be complex (Watt and Fogg 1966; Dunstall 1974; Smith 1974; Nalewajko et al. 1976), and a variety of patterns have been observed in the few studies on natural phytoplankton populations (Fogg et al. 1965; Watt 1966; Nalewajko and Marin 1969). Therefore one objective of this work was to investigate more thoroughly the kinetics of extracellular release in phytoplankton.

Two lakes in the Experimental Lakes Area, northwestern Ontario, were selected for study. Previously, Schindler and Holmgren (1971) concluded that excretion was negligible in a number of lakes in the ELA, amounting to less than 1% of the total ^{14}C fixed. However, they applied a

Printed in Canada (J3683)
Imprimé au Canada (J3683)

correction for "filtration error" (Arthur and Rigler 1967). Subsequently, an explanation not involving cell breakage was proposed to account for the decreasing radioactivity per milliliter on filters with increasing volume filtered (Nalewajko and Lean 1972a; McMahon 1973) and a correction for filtration error no longer appears valid. In more recent work, total primary production (particulate and extracellular) was measured in ELA lakes, using a method not involving filtration (Schindler et al. 1972), but the extent of extracellular release was not determined. Therefore our second objective was to test whether p.e.r. values in a softwater, oligotrophic lake, and in the artificially eutrophic Lake 227 conform to the values reported in other lakes (Fogg 1966; 1971).

Our third objective was to assess the extent of the flow of DOC from phytoplankton to heterotrophs. Undoubtedly, heterotrophs in aquatic systems are capable of utilizing phytoplankton products (Fogg 1966), but quantitative data are lacking. Saunders and Storch (1971) have shown that bacteria can be extremely dependent on algal extracellular DOC. Conversely, Saunders (1972) concluded that algal extracellular products are a less important source of DOC than organic detritus. Since even in short-term experiments a variety of substances are excreted, ranging from simple organic acids and sugars to complex polysaccharides and polypeptides (Fogg 1971; Hellebust 1974), it is not possible to estimate heterotrophic utilization rates of all these. Without assuming that glucose, acetate, or glycollate are the major extracellular products, it seemed valid to use these three to estimate the heterotrophic utilization capacity for small molecules. The rationale here is that if extracellular release rates exceed or equal uptake rates of these substances (Wright 1970), then phytoplankton are likely to be a major source of DOC for heterotrophs. If extracellular release rates are much lower than heterotrophic uptake, then other DOC sources must be important.

Methods

Primary Production and Extracellular Release

40 μ Ci of carrier-free $NaH^{14}CO_3$ were added to epilimnion lake water in 125-ml pyrex bottles. Bottles were rotated in a light incubator (Fee 1973) at the prevailing epilimnion temperature, and at two or four representative light intensities. Samples were equilibrated for 1 h in the incubator before ^{14}C was added. After incubation, particulate and extracellular production was measured by filtering 10- or 15-ml aliquots on 0.45-μ membrane filters using gentle suction (75 mm Hg). The filtrates were acidified to pH 3.5 and aerated for 20 min. Radioactivity of filtrates and filters was measured in a Beckman Scintillation Counter. A dioxane base fluor was used for counting (Schindler and Holmgren 1971).

Dissolved inorganic carbon (DIC) in lake water was measured by gas chromatography (Stainton 1973).

Sephadex G-15 in 45 cm $\times$ 2.5 cm columns was used to estimate the molecular weight of ^{14}C organic compounds in filtrates from primary production experiments (Nalewajko and Lean 1972b). Fractions of 3.5–4.0 ml were collected in scintillation vials and counted after addition of the dioxane base fluor.

Uptake of Organic Compounds

In experiments on uptake of organic compounds, sodium acetate ^{14}C (62 mCi/mmol) and glucose-^{14}C (268 mCi/mmol) were used after dilution to the required concentrations. Lake water samples in Pyrex bottles were incubated at constant temperature, in low light (0.003 ly min^{-1}) and were agitated to ensure mixing. Uptake was followed by filtering 10-ml aliquots on 0.45-μ membrane filters at intervals for about 2 h. The radioactivity of the filters was determined using methods outlined above. At each ^{14}C substrate concentration, rates of uptake by the particulate fraction were corrected for respiratory $^{14}CO_2$ losses by acidifying to pH 3.5 and aerating samples before and after experiments. Rate constants (k, in min^{-1}) of ^{14}C substrate uptake were calculated from regressions of ln percent radioactivity in the filtrate against time. At each substrate concentration (C, in micrograms C $liter^{-1}$) rate of uptake (V, in micrograms C $liter^{-1}$ min^{-1}) was calculated as $V = kC$.

Two techniques were used to estimate natural concentrations of organic substrates (S_n) in lake water. The first was the "dilution" bioassay of Allen (1968). The other was the "tracer" bioassay technique used by Rigler (1966) to estimate orthophosphate concentrations.

Results

Primary Production and Extracellular Release

Uptake of ^{14}C by Lake 227 phytoplankton was linear at each of the four light intensities over the experimental period (Fig. 1; July 31). Saturation was approached at 0.05–0.15 ly min^{-1} (Fig. 3). Extracellular release rates changed during the experiment, but the change was not appreciable at the two lowest intensities. In the first samples, 10–13 min after the addition of ^{14}C, appreciable quantities of extracellular products were already present (Fig. 1). From that point to about 60 min, extracellular release rates at each light intensity were constant, and increased with increasing light intensity. At about 60 min, excretion rates changed to higher values and remained constant until the experiment was terminated 2 h later. These final excretion rates also increased with light intensity (Fig. 2) and showed a steeper

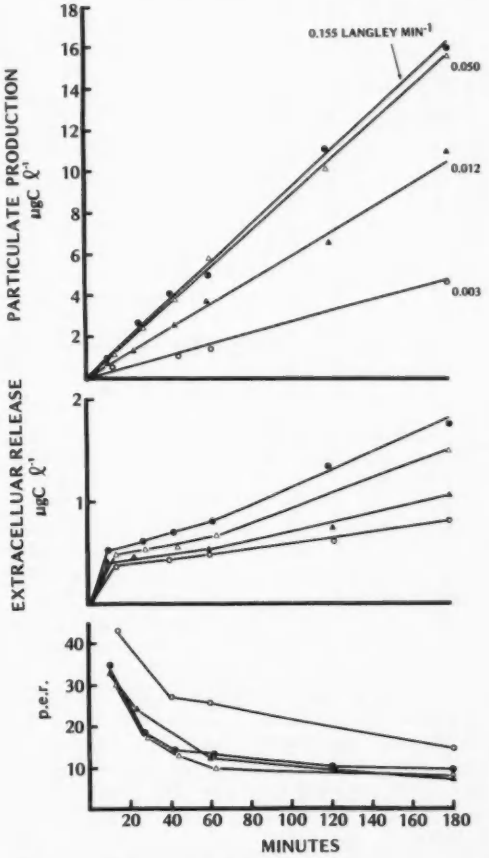

FIG. 1. Primary production, extracellular release and percentage extracellular release (p.e.r.) in Lake 227, July 31, 1973, at four light intensities.

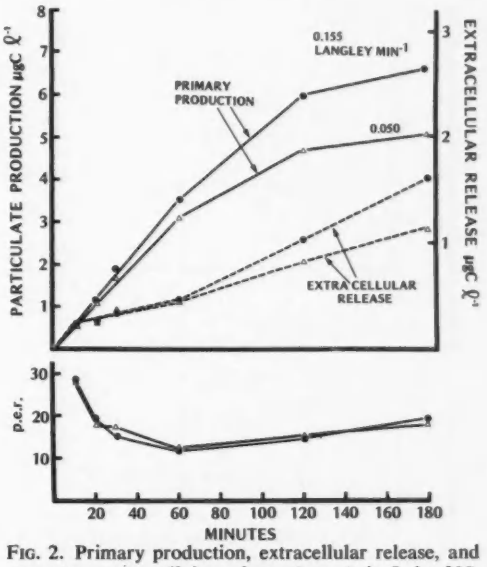

FIG. 2. Primary production, extracellular release, and percentage extracellular release (p.e.r.) in Lake 239, July 25, 1973, at two light intensities.

increase between 0.05 and 0.15 ly min^{-1} than seen in the photosynthetic rates.

This experiment was repeated on August 10. Between July 31 and August 10 epilimnetic chlorophyll increased from 12.1 to 26 μg $liter^{-1}$, because of increased phytoplankton populations. *Oscillatoria redeckii* was the dominant species in the phytoplankton bloom. Primary production rates increased about tenfold but extracellular release rates were only about 3–4 times higher on August 10 than on July 31. However, the kinetics of primary production and extracellular release were essentially identical to the previous experiment. Values for p.e.r. ranged from 43 to about 8% when phytoplankton density was low (July 31), but were much lower, ranging from 11 to 1%, at high population density (August 10). A marked decrease of p.e.r. values was observed from about 10 to 60 min.

Primary production and excretion rates of Lake 239 phytoplankton were measured at only two light intensities (Fig. 2). Photosynthesis rates were constant for 60 min, then declined. The 10-min filtrates contained an appreciable quantity of extracellular products. From 10 to 60 min, extracellular release rates were constant, then changed to higher rates which remained constant till 180 min. Percent extracellular release ranged from about 30% at 10 min to 12% at 3 h.

In both lakes, the ^{14}C labelled extracellular material mostly had molecular weights greater than 1500, as shown by Sephadex gel filtration (Fig. 4 and 5). Small molecular weight material represented less than 10% of total extracellular products in all cases, even after incubation times of only 1 h. It appears that either only large molecules were excreted in the period between 1 and 3 h, or any small molecules excreted were consumed by bacteria and other heterotrophs.

Concentrations and Uptake of Labeled Organic Substances

The time course of removal of ^{14}C acetate and glucose from solution by the particulate fraction can be described by decreasing exponential curves. Rate constants calculated for each concentration were used to obtain rates of uptake for the dilution and the tracer bioassay plots.

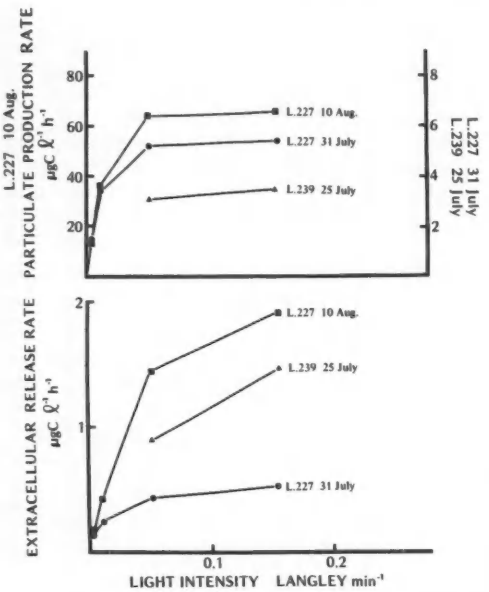
L.227 10 Aug. PARTICULATE PRODUCTION RATE µgC l⁻¹ h⁻¹
L.227 31 July L.239 25 July
L.227 10 Aug.
L.227 31 July
L.239 25 July
EXTRACELLULAR RELEASE RATE µgC l⁻¹ h⁻¹
L.227 10 Aug.
L.239 25 July
L.227 31 July
LIGHT INTENSITY LANGLEY min⁻¹

FIG. 3. Rates of primary production and extracellular release in relation to light intensity.

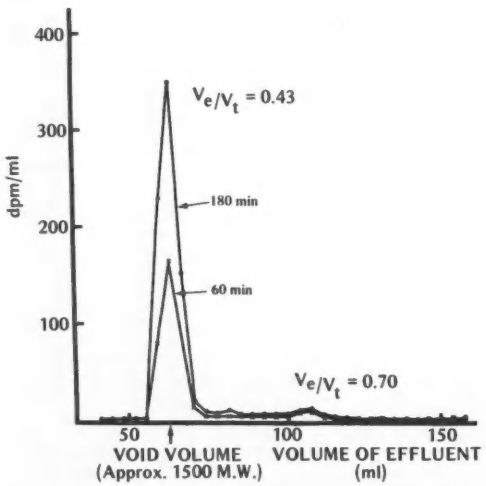

FIG. 4. Sephadex gel fractionation of acidified and bubbled filtrates after 60 min and 180 min incubation with ^{14}C, 0.1546 ly min^{-1}, Lake 239, July 25.

A dilution bioassay for acetate in Lake 227 (August 13), using double-distilled water as a dilution medium, gave nonsolvable kinetics of a type not encountered by Allen (1968). V_{max} (Table 1) for the diluted series was only about

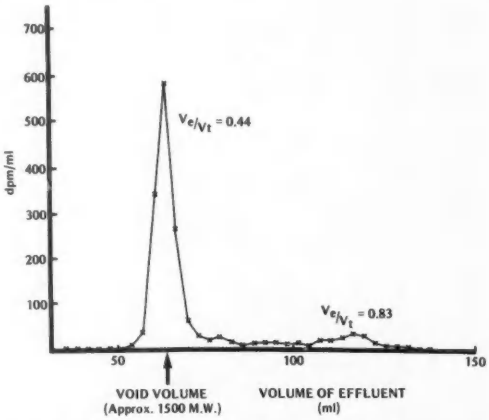

FIG. 5. Sephadex gel fractionation of filtrates after 180 min incubation with ^{14}C, 0.1546 ly min^{-1}, Lake 227, August 10.

20% of the value in undiluted samples instead of the expected 50%, indicating that some sort of physiological shock was imposed by the dilution procedure.

The tracer bioassay procedure applied on the same date gave a maximum probable acetate concentration (S_n) of 0.2 μg liter^{-1} (Fig. 6).

Dilution bioassays for glucose in Lake 227 (August 15) gave peculiar results, with V_t in the diluted series only 30% of that in the undiluted set. The tracer bioassay gave a concentration estimate of 1.0 μg liter^{-1} (Fig. 7). Data for the oligotrophic Lake 239 are shown in Fig. 8 and in Table 1.

Rate constants for uptake of glucose and acetate were extremely low. Using the estimates of natural substrate concentrations from tracer bioassays, uptake rates of the two substances, corrected for respiration, were calculated for comparison with the rates of extracellular release (Table 1).

Discussion

Our data show the importance of following the time course of both particulate production and extracellular release, since rates of both may change even during relatively short experiments. Excretion rates increased significantly at the two highest light intensities after 1 h. Increased excretion rates, in the absence of changed photosynthetic rates, may be attributed to the appearance of new ^{14}C extracellular products derived from later metabolic pathways, that is, Type II substances (Fogg 1966). A similar change has been observed after about 3 h incubation with

TABLE 1. Dilution bioassay and tracer bioassay for acetate and glucose in lakes 227 and 239. (K_t, transport constant; S_n, natural substrate concentration; V_{max}, maximum uptake velocity.)

			Michaelis–Menten parameters					Tracer bioassay	
			Control		Diluted				
Lake	Date	Organic compound	$K_t + S_n$ ($\mu g\ liter^{-1}$)	V_{max} ($liter^{-1}\ h^{-1}$)	$K_t + \frac{S_n}{2}$	$\frac{V_{max}}{2}$	S_n ($\mu g\ liter^{-1}$)	Concn (max) ($\mu g\ liter^{-1}$)	Uptake rate, corrected for respiration at natural substrate concns ($\mu g\ C\ liter^{-1}\ h^{-1}$)
L.227	Aug. 6	Acetate	12.8 (14.9)[a]	20.6 (6.9)	—	—	—	0.3	0.087
	Aug. 13	Acetate	9.3 (5.2)	20.8 (8.8)	0.95 (0.36)	3.9 (2.1)	—	0.2	0.061
	Aug. 15	Glucose	5.2 (10.2)	14.5 (11.2)	2.98 (5.5)	4.0 (3.0)	4.5 (9.4)	1.0	0.481
L.239	Aug. 7	Acetate	2.6	0.54	—	—	—	0.5	0.042

[a]All values in parentheses were calculated from uptake data without a respiration correction.

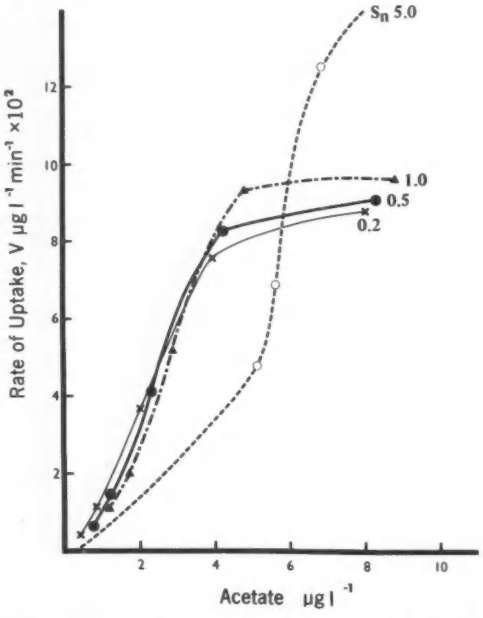

FIG. 6. Tracer bioassay for acetate in Lake 227, August 13.

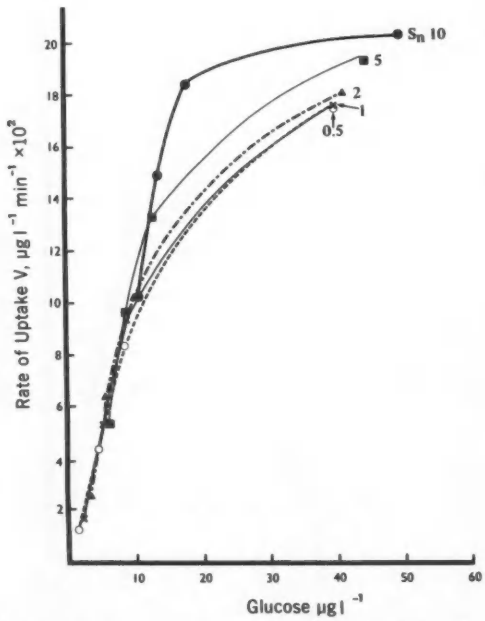

FIG. 7. Tracer bioassay for glucose in Lake 227, August 15.

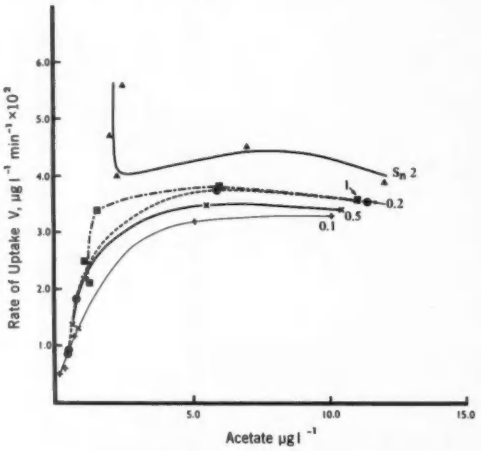

FIG. 8. Tracer bioassay for acetate in Lake 239, August 7.

^{14}C in cultures of *Anabaena flosaquae* (Nalewajko et al. 1976). In Lake 239, increased excretion rates accompanied by decreased photosynthesis could be partly a result of CO_2 limitation (Nalewajko 1966). Dissolved inorganic carbon (DIC) concentrations in this lake were only 115 μM on July 24, compared to 358 μM in Lake 227 on July 31 with a comparable phytoplankton biomass. Schindler and Fee (1973) demonstrated CO_2 limitation of photosynthesis in Lake 227 during 2 summer months because of a midday DIC shortage.

Our experiments indicate that appreciable amounts of DOC are excreted by phytoplankton, especially in Lake 227. Relative excretion, that is p.e.r., showed an inverse relation to phytoplankton biomass (Watt 1966). In both lakes, 90% of the extracellular material found after 1–3 h had molecular weights higher than 1500. A similar observation was previously made in several other lakes (Nalewajko and Lean 1972b) in which the molecular weight of the major portion of extracellular products probably exceeds 5000. Although direct comparisons cannot be made, it is interesting that in exponential phase axenic cultures of algae small molecules are relatively more abundant in short-term experiments; large molecules become predominant in older cultures, and in mixed algal–bacterial cultures (Nalewajko and Lean 1972b; Nalewajko et al. 1976; Dunstall and Nalewajko 1976).

One possible explanation for low amounts of small molecules in phytoplankton excretion products is that they are rapidly consumed by heterotrophs, thus allowing no buildup to occur.

Extensive evidence exists that bacteria utilize algal excretion products (Nalewajko 1976). It is likely that low molecular weight extracellular products are rapidly removed in lakes, matching the rates of glycollate, glucose, and acetate utilization (Wright and Hobbie 1966; Wright 1970). As a result, true or "gross' excretion rates of phytoplankton will be underestimated in the presence of some heterotrophs.

Wright (1970), in a series of simultaneous extracellular release and heterotrophy experiments, demonstrated a close correlation between DOC excretion by phytoplankton and V_{max} values for glycollate in the photic zone. While V_{max} is undoubtedly a useful measure of potential heterotrophic glycollate uptake, it should show such a close correlation with excretion rates only if glycollate was the predominant extracellular product. We failed to detect glycollate in Lake 239 or Lake 227, while small amounts may have been present in one out of four lakes in another study (Nalewajko and Lean 1972b). Others have also shown that glycollate is seldom the predominant substance in filtrates from short-term ^{14}C primary production experiments (Watt 1966; Hellebust 1974). However, it is possible that glycollate and other small molecules are in fact major extracellular products which are removed very rapidly by heterotrophs, as discussed earlier. The close correspondence of "net" extracellular release rates (probably referring to the production of predominantly large molecules) and V_{max} values for glycollate in Gravel Pond (Wright 1970) must be a coincidence. In our experiments, V_{max} values for acetate in Lake 227, August 10, were higher than for glucose. Both exceeded by about threefold the maximum total carbon excreted. Perhaps if gross excretion rates were known, the V_{max} and excretion rates may have been closer. In Lake 239, V_{max} for acetate was very much lower than in Lake 227 and amounted to only about one seventh of the maximum excretion rate.

Direct measurements of heterotrophic uptake rates, using natural substrate concentrations determined by the tracer bioassays, were much lower than V_{max} values for the same substance. For example, in Lake 227, on August 10 extracellular release (net) at the highest light intensity was 1.92 μg C liter^{-1} h^{-1}. Glucose and acetate uptake values corrected for respiration, were 0.481 and 0.061 μg C liter^{-1} h^{-1}, respectively. It was not possible to estimate glycollate concentrations, but at 1.6 μg liter^{-1} glycollate, the uptake rate was 0.11 μg C liter^{-1} h^{-1}. Total heterotrophic uptake of glucose, acetate, and glycollate was therefore 0.652 μg C liter^{-1} h^{-1}. While we realize that these three substances are not necessarily the only, or even the major algal excretion products, the rates of their utilization may give some idea of the size of the "missing" low molecular weight portion of algal extracellular products. In this case gross extracellular release could have been 2.572 μg C liter^{-1} h^{-1}, while the measured net excretion was only 1.92 μg C liter^{-1} h^{-1}. Ideally, compounds known to be excreted by the algae present in the phytoplankton assemblage should be used. At present this is difficult because extracellular products have been identified in only a few planktonic algae, and because reliable direct methods for estimating natural concentrations of individual organic substances are lacking. The tracer bioassay (Rigler 1966) which estimates only the maximum substrate concentrations proved to be more reliable here than the dilution bioassay of Allen (1968). Values for acetate and glucose obtained by the tracer bioassay method were substantially lower than $K_t + S_n$ values from the Michaelis–Menten analysis. Errors have been minimized by calculating uptake rates from rate constants over a 1–2 h period, rather than from replicate determinations of uptake at one time only, which is the accepted procedure. However, the choice of the "acceptable" assumed S_n value is somewhat arbitrary. For example, in Fig. 6, while an S_n value of 5 μg liter^{-1} is clearly unacceptable, the decision as to whether 0.2 μg liter^{-1} or 0.5 μg liter^{-1} is the more acceptable value is not so clear cut. However, in view of objections raised on mathematical grounds to certain aspects of the Michaelis–Menten analysis (Riggs 1963), an estimate of S_n from the tracer bioassay involves fewer assumptions, and appears preferable to $K_t + S_n$ estimates from the Michaelis–Menten analysis.

Acknowledgments

This research was carried out during C.N.'s sabbatical leave and was made possible through financial support from the Fisheries Research Board. I thank Dr R. D. Hamilton, Dr E. Fee, Mr M. Turner, Miss S. Levine, and many others among the staff and students at the ELA camp for their generous help.

ALLEN, H. L. 1968. Acetate in fresh water: natural substrate concentrations determined by dilution bioassay. Ecology 49: 346–349.

ARTHUR, C. R., AND F. H. RIGLER. 1967. A possible source of error in the ^{14}C method of measuring primary productivity. Limnol. Oceanogr. 12: 121–124.

DUNSTALL, T. 1974. Extracellular release in planktonic algae and bacteria. M.Sc. Thesis. Univ. Toronto, Toronto, Ont. 000 p.

DUNSTALL, T., AND C. NALEWAJKO. Extracellular release in bacteria. Verh. Int. Ver. Limnol. (In press)

FEE, E. J. 1973. A numerical model for determining integral primary production and its application to Lake Michigan. J. Fish. Res. Board Can. 30: 1447–1468.

FOGG, G. E. 1966. The extracellular products of algae. Oceanogr. Mar. Biol. Annu. Rev. 4: 195–212.

1971. Extracellular products of algae in freshwater. Arch. Hydrobiol. Beih. 5: 1–25.

FOGG, G. E., C. NALEWAJKO, AND W. D. WATT. 1965. Extracellular products of phytoplankton photosynthesis. Proc. R. Soc. London, Ser. B 162: 517–34.

HELLEBUST, J. A. 1974. Extracellular products, p. 838. *In* W. D. P. Stewart [ed.] Algal physiology and biochemistry. Botanical monographs 10. Blackwell Scientific Publications,

MCMAHON, J. W. 1973. Membrane filter retention — a source of error in the ^{14}C method of measuring primary production. Limnol. Oceanogr. 18: 319–324.

NALEWAJKO, C. 1966. Photosynthesis and excretion in various planktonic algae. Limnol. Oceanogr. 11: 1–10.

1976. Extracellular release in freshwater algae and bacteria: extracellular products of algae as a source of carbon for heterotrophs. *In* J. Cairns Jr. [ed.] The Aquatic microbial communities. Marcel Dekker, Inc., New York, N.Y. (In press)

NALEWAJKO, C., T. G. DUNSTALL, AND H. SHEAR. 1976. Kinetics of extracellular release in axenic algae and in mixed algal: bacterial cultures; significance in estimation of total (gross) phytoplankton excretion rates. J. Phycol. (In press)

NALEWAJKO, C., AND D. R. S. LEAN. 1972a. Retention of dissolved compounds by membrane filters as an error in the ^{14}C method of primary production measurements. J. Phycol. 8: 37–43.

1972b. Growth and excretion in planktonic algae and bacteria. J. Phycol. 8: 361–366.

NALEWAJKO, C., AND L. MARIN. 1969. Extracellular production in relation to growth of four planktonic algae and of phytoplankton populations from Lake Ontario. Can. J. Bot. 47: 405–413.

RIGGS, D. S. 1963. The mathematical approach to physiological problems. Massachusetts Institute of Technology Press, Cambridge, Mass. 445 p.

RIGLER, F. 1966. Radiobiological analysis of inorganic phosphorus in lake water. Verh. Int. Ver. Limnol. 16: 465–470.

SAUNDERS, G. W. 1972. The transformation of artificial detritus in lake water. Mem. Ist ital. Idrobiol. 29: Suppl. 261–288.

SAUNDERS, G. W., AND T. A. STORCH. 1971. Coupled oscillatory control mechanism in a planktonic system. Nature (London) 230: 58–60.

SCHINDLER, D. W., AND E. J. FEE. 1973. Diurnal variation of dissolved inorganic carbon and its use in estimating primary production and CO_2 invation in L. 227. J. Fish. Res. Board Can. 30: 1501–1510.

SCHINDLER, D. W., AND S. K. HOLMGREN. 1971. Primary production and phytoplankton in the Experimental Lakes Area, Northwestern Ontario, and other low-carbonate waters and a liquid scintillation method for determining ^{14}C activity in photosynthesis. J. Fish. Res. Board Can. 28: 189–201.

SCHINDLER, D. W., R. V. SCHMIDT, AND R. A. REID. 1972. Acidification and bubbling as an alternative to filtration in determining phytoplankton production by the ^{14}C method. J. Fish. Res. Board Can. 29: 1627–1631.

SMITH, W. V. JR. 1974. The extracellular release of glycollic acid by a marine diatom. J. Phycol. 10: 30–33.

STAINTON, M. P. 1973. A syringe gas-stripping procedure for gas-chromatographic determination of dissolved inorganic and organic carbon in fresh water and carbonates in sediments. J. Fish. Res. Board Can. 30: 1441–1445.

WATT, W. D. 1966. Release of dissolved organic material from the cells of phytoplankton populations. Proc. R. Soc. London Ser. B 164: 521–551.

WATT, W. D., AND G. E. FOGG. 1966. The kinetics of extracellular glycollate production by *Chlorella pyrenoidosa*. J. Exp. Bot. 17: 117–134.

WRIGHT, R. T. 1970. Glycollic acid uptake by planktonic bacteria, p. 521–536. *In* D. W. Hood [ed.] Organic matter in natural waters. Publ. 1. Inst. Mar. Sci., Univ. Alaska, College, Alaska.

WRIGHT, R. T., AND J. E. HOBBIE. 1966. The use of glucose and acetate by bacteria and algae in aquatic ecosystems. Ecology 47: 447–464.

Ecology of Chironomidae (Diptera) in a Polar Lake[1]

H. E. WELCH

Department of the Environment, Fisheries and Marine Service, Biological Station, St. Andrews, N.B. E0G 2X0

WELCH, H. E. 1976. Ecology of Chironomidae (Diptera) in a polar lake. J. Fish. Res. Board Can. 33: 227–247.

The six common genera of Chironomidae (Diptera) in Char Lake, Resolute, Northwest Territories (74°42'N lat.) were studied intensively from 1969 to 1972. *Heterotrissocladius oliveri* and a *Trissocladius* species are characteristic of the sediment zone, while two species of *Orthocladius*, *Pseudodiamesa arctica*, *Paracladius quadrinodosus*, and *Lauterbornia* sp. are restricted mainly to the rocky and moss zones. Life cycles are 2 or 3 yr, depending upon the species. Year-classes could be discriminated by instar frequency distribution. Populations increased steadily during the study period, for an average increase in strength of 5 times between the 1968 and 1971 year-classes. Summer emergence and egg-laying conditions are of overriding importance to year-class strength. Mortality within year-classes is undetectable until the last 4 mo of larval life, when mortality due to char predation is about 65% between April and the time of emergence. The physiology of these chironomids does not seem unusual aside from continuing activity down to 0 C, and there is no indication of metabolic compensation. Net growth efficiency averages 36%. Assimilated energy (growth + respiration) at 8.6 kcal m^{-2} yr^{-1} is very low compared with temperate zone populations, but is more similar as a percent of photosynthesis, 4.1%. The relatively large detritus pool and the presence of both 2- and 3-yr species tend to stabilize chironomid energy flow. Definition of long-term averages for chironomid populations in Char Lake would require a decade or more of study.

WELCH, H. E. 1976. Ecology of Chironomidae (Diptera) in a polar lake. J. Fish. Res. Board Can. 33: 227–247.

Nous avons étudié intensivement les six genres communs de Chironomidae (Diptera) du lac Char, Resolute, Territoires du Nord-Ouest (74°42' lat.N) de 1969 à 1972. *Heterotrissocladius oliveri* et une espèce de *Trissocladius* sont caractéristiques du zone de sediments, tandis que deux espèces d'*Orthocladius*, de *Pseudodiamesa arctica*, de *Paracladius quadrinodosus*, et de *Lauterbornia* sp. sont caractéristiques principalement des zones de roches et de mousse. Les cycles biologiques sont de 2 ou 3 ans, selon l'espèce. Les classes annuelles peuvent être séparées par la distribution de fréquence des instars. Les populations ont augmenté régulièrement durant la période d'étude, avec une augmentation d'abondance moyenne de 5 fois de la classe de 1968 à celle de 1971. L'émergence en été et les conditions d'oviposition sont d'importance capitale pour le succès d'une classe annuelle. La mortalité au sein des classes annuelles ne peut être décelée avant les 4 derniers mois de vie larvaire, alors que la mortalité due à la prédation par l'omble chevalier est d'environ 65% entre avril et la période d'émergence. La physiologie de ces chironomides ne semble avoir rien d'insolite, si ce n'est que l'activité se poursuit jusqu'à 0 C et qu'il n'y a pas de preuve de compensation métabolique. L'efficacité de croissance nette est de 36% en moyenne. L'énergie assimilée (croissance + respiration) à 8.6 cal m^{-2} an^{-1} est très faible comparativement à celle des populations de la zone tempérée, mais s'en rapproche davantage lorsque exprimée en pourcentage de photosynthèse, 4.1%. Le pool de déchets relativement grand et la présence d'espèces de 2 et 3 ans tendent à stabiliser le flux énergétique des chironomides. Une définition de moyennes à long terme pour les populations de chironomides du lac Char exigerait 10 années d'études ou plus.

Received May 30, 1975
Accepted November 12, 1975

Reçu le 30 mai 1975
Accepté le 12 novembre 1975

THE CCIBP Char Lake project was a cooperative study of energy flow in a Canadian high arctic lake at Resolute, Northwest Territories (74° 42′ N). Project background and description of the lake were given by Rigler (1972), and Char Lake's physical and chemical limnology was discussed by Schindler et al. (1974). The present paper reports further investigations of the Chironomidae (Diptera), complementing a previous paper on chironomid emergence (Welch 1973). My chief aim here is to elucidate the energy flow through the chironomids, which of

[1]Canadian Committee for the International Biological Programme Contribution No. 274 and Char Lake Project Contribution No. 24.

Printed in Canada (J3850)
Imprimé au Canada (J3850)

course depends heavily on their life histories and general biology; however, these autecological aspects are not discussed in great detail.

There are seven common species of chironomids in Char Lake. *Pseudodiamesa arctica* (Mall.), *Heterotrissocladius oliveri* Sæth. (Sæther 1975) (*H. subpilosus* in Welch 1973), and *Trissocladius* sp. nov.[2] are abundant. *Orthocladius lapponicus* (Goetgh.) is found in the moss zone, and another *Orthocladius* species is common in the rocky zone, but they are not separated herein. *Lauterbornia* sp. nov.[2] are parthenogenetic. A very small population of *Paracladius quadrinodosus* (Hirv.) (*Cricotopus alpicola* in Welch 1973) was also present.

Methods

The numbers of larvae in each genus were quantified over space and time by an intensive sampling program. Growth curves could be constructed for each genus since year-classes could be distinguished by instar frequency distribution. Laboratory studies were made on respiration, calorific values, and dry weight. Observations of egg-laying, time of pupation, etc. completed life-history determinations, and the data were then integrated to obtain population energy flow.

The energy budgets discussed here are modeled upon:

$$\text{Ingestion} = \text{Growth} + \text{Respiration} + \text{Egestion} \quad (1)$$

Char Lake chironomids are detritivores (Davies 1974) and their assimilation efficiencies $\frac{G+R}{I}$ are very low (M. N. Charlton personal communication). Because egested energy (E) remains in the detritus food pool, assimilated energy (G + R) is more meaningful than ingested energy (I) when discussing detritivores (Welch 1968), and growth and respiration are far easier to measure than ingestion, egestion, or assimilated efficiency. Hence for Char Lake chironomids, I determined only growth and respiration, from which assimilated energy and net growth efficiency $\frac{G}{G+R}$ were derived.

Field Samples

Sediment zone — Different methods were required to sample quantitatively the three distinct bottom types found in Char Lake (Fig. 1 and 2). The sediment zone below the moss was cored at 3-mo intervals (January, April, July, and October) from April 1970 through April 1972, at transect A, with a weighted four-head corer (Hamilton et al. 1970). Three drops, 1–2 m apart, were made at about 2-m intervals from 25 to 15 m depth. In July 1972, the sediment zone was cored at 42 random locations to determine the horizontal distribution of larvae. Lastly, 18 core samples were taken from a depth of 16 m at transect A on July 18, 1973, to determine the 1972 year-class strength of *Trissocladius* and *Heterotrissocladius*.

[2]New species being described by D. R. Oliver.

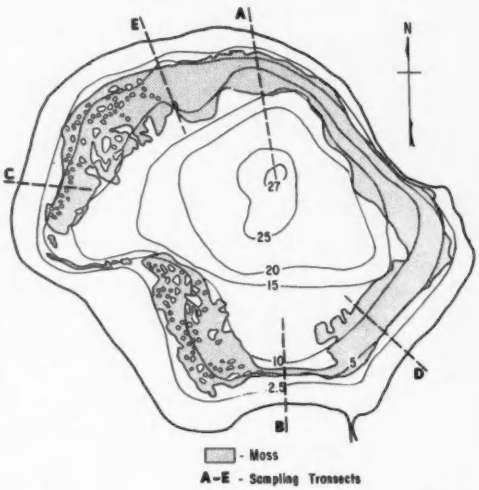

FIG. 1. Char Lake showing chironomid sampling transects.

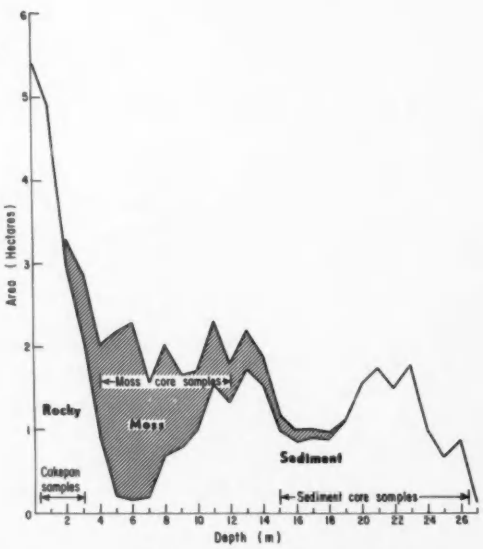

FIG. 2. Areas of bottom types in Char Lake, and distribution of quantitative sampling types. Area of the rocky zone is 15.41 ha (0–4 m of the nonmoss area), and area of the sediment zone is 22.59 ha (8–27 m of the nonmoss area).

When coring, the corer was lowered from the ice surface into the mud at less than 10 cm s^{-1}, and the 60 cm × 5.17 cm inside diameter (ID) steel core tubes allowed to penetrate vertically until the cable slackened slightly; some tension was maintained to prevent the corer from tipping over on firm substrate. Divers reported the complete absence of a pressure wave preceding the core tubes. After sealing, the corer was drawn to the surface and the bottom of the core tubes stoppered. Each core tube was removed, the overlying water and surface sediment poured from the top of the core tube through a 67-μ screen, and a wash bottle used to remove the entire brown oxidized zone containing the larvae. Tests showed that the deeper, grayer, and more compact sediment contained no larvae. The sample was then washed into a pharmaceutical cylinder containing a sugar solution, stirred, and left for 5 min, after which the heavy sediment was drained and discarded through a tube in the bottom of the cylinder. The floated material was then drained off through a 67-μ screen, washed, and preserved with formalin for subsequent sorting.

The November 1971 and January 1972 series were not sugar-floated in the field, but were preserved immediately. These samples were subsequently "crushed" before sorting by running a foam-neoprene roller over them in a trough. The sediment in Char Lake is almost entirely aggregated into chironomid fecal pellets which are readily fragmented into the component silts, and, after crushing, nearly all the inorganic material passes through a 67-μ screen. Crushing was nearly as efficient as sugar flotation as an aid to sorting. About 2 days were required to sort the animals from the oxidized sediment of a core sample, whereas a floated or crushed sample could be sorted in 1–2 h.

Moss zone — The moss zone was sampled with a 19.5-cm ID plexiglass cylinder with 67-μ screening over one end. A diver would locate the desired depth with a marked line and float (beneath the ice), then push the corer deeply into the moss, reach below the corer and cover the bottom with one hand, and return to the diving hole, where the contents were poured into pails and returned to the lab. Within 24 h the moss from each sample was removed, placed in a tank of ice water, and aerated vigorously while cold water was circulated through the tank. The overflow passed through a coarse screen which retained most of the moss, but allowed animals to go through to be collected in a 67-μ screen. Each sample was extracted for four 1-h periods, and the collected material floated and preserved for sorting. The water and mud remaining in the container, from which the moss had been removed, was also screened, floated, and preserved.

Samples were taken at 3-mo intervals from July 1971 through July 1972 at 2 m depth intervals, covering the range of moss from 4–5 m to 14–15 m, on transect A. Also in July 1972, moss samples were taken at 2-m intervals from areas D and E.

Rocky zone — The 0–3 m deep rocky zone consists of small rocks, and grades from relatively sediment-free, wave-washed rock at the shore, down to rocks lightly covered with fine sediment and filamentous algae at 2–3 m. This zone was sampled by placing 21.5 cm I.D. × 2.5 cm deep aluminum cake pans into the substrate, with their rims flush or slightly below the sediment surface, and filling the pan with the material from the hole. Upon being removed 1 or 2 yr later, each pan was grasped carefully by the rim, lifted free of the substrate, and a 67-μ stainless steel mesh bag swept around the sample and returned to shore. Each sample was washed several times with a vigorous stream of water, and the fine sediment and organic material were then poured off through a 67-μ screen, sugar-floated, and preserved. No larvae remained on the cleaned rocks or coarse material.

Cake pans, placed in late August 1969 on transect A, were removed from the rocky zone on August 7–8 and September 8–9 of 1970, two pans each time from 0.5, 1, 2, and 3 m depth. Pans placed in 1970 were removed between July 19 and 27, 1971, two pans per depth, at transect A, and four pans per depth at transect B and at transect C.

Efficiency tests — Flotation efficiency was determined by sorting the sediment portion of each sugar-floated sample for the July 1970 and July 1971 sediment-core series, and the summer 1971 rocky zone cake-pan series. Results (Table 1) showed that for *Trissocladius* and *Heterotrissocladius* instars I–IV, the flotation process for sediment-core samples was 98% efficient, and for cake-pan samples, which contained more sediment and filamentous algae, 78% efficient. Pupae of all species were floated with 70% efficiency for cores and 67% for cake pans, probably because pupae were often enclosed in a pupal case comprised of silt particles. *Lauterbornia* instars I–IV were floated with 50% efficiency for cores and 58% efficiency for cake pans, because the tube-dwelling larvae often remained in their tubes of cemented silt and did not float. When the raw sorting data were corrected for these efficiencies (see below), I used the average flotation efficiency of 69% for pupae and 58% for *Lauterbornia* larvae for both cake-pan and core samples. No significant differences were found between instars II–IV for any species, while not enough instar I were found to warrant analysis.

The moss elutriation technique removed 95% of the larvae in the moss taken from the sample container, with 77% of the larvae removed in the first hour and a further 11, 7, and 5% removed after 2, 3, and 4 h. There was no difference between instars. Half the total larvae in the sample were left in the residue in the sample container after the moss had been removed. The flotation method used on both the residues and the elutriated material was not separately tested, the flotation efficiency being assumed the same as for sediment cores.

Sorting efficiency was determined for several technicians by resorting 10 core and 6 cake-pan samples. No significant differences were found between workers or between larval stages. The overall picking efficiency for instars II–IV was 92% (Table 2). The data were, therefore, corrected upwards in this

TABLE 1. Efficiency of sugar flotation for cores and cake-pan samples.

Kind of sample	No. of samples checked	Genus	Instar	Total no. in sediment portions	Total no. in whole samples	Not floated (%)
Core	111	*Trissocladius* *Heterotrissocladius*	I–IV	25	1332	1.9
Cake-pan	10	*Heterotrissocladius* *Orthocladius*	I–IV	205	945	21.7
Core	87	*Lauterbornia*	I–IV	3	6	50.0
cake-pan	34			22	53	41.5
Core	87	*Trissocladius*, *Heterotrissocladius*, and *Orthocladius*	Pupae	8	26	30.1
cake-pan	34			3	9	33.3

TABLE 2. Sorting efficiency for 10 core and 6 cake-pan samples.

Instar	I	II	III	IV	Pupae
Numbers in first sorting	35	325	93	114	7
Numbers in resorting	1	29	8	10	3
% in resorting	2.7	8.2	7.9	8.1	42.9

sequence, where applicable: number of chironomids in a sample was divided first by extraction efficiency, then flotation efficiency, then sorting efficiency.

Estimating total populations — There was no correlation of larval numbers with depth in the sediment zone (see Results), so numbers m^{-2} in each instar at each sampling period were multiplied by the area of the sediment zone. Larval numbers were, however, related to depth within the moss and rocky zones, and numbers of larvae at each sampling period were integrated at 1-m intervals accordingly. This left 2.00 ha (3.8% of the total area) as patches of sediment in the moss. These patches go anaerobic over winter (Welch and Kalff 1974), and a series of core samples I took from them early in July 1971 showed that almost no larvae were living in them at that time, so these patches are not included in further calculations.

The total number of larvae in each instar was summed for all three zones and divided by the lake area to give numbers m^{-2} of lake surface at each sampling period. Each instar was then placed in a year-class according to Fig. 5 (see Results) to give population estimates for every year-class for each species at 3-mo intervals. Because quantitative sampling began in January 1970, I could obtain estimates for the 1967, 1968, and 1969 year-classes for the 3-yr species, the 1968 and 1969 year-classes for the 2-yr species, and the 1970 and 1971 year-classes for all species.

GROWTH

The general growth pattern is, of course, determined by the life history of each species as outlined in Fig. 5 in the Results section. Dry weight determinations were made on each instar and species at times when each year-class was largely or entirely of one instar, as for example, in March when all second instar *Trissocladius* belong to the year-class hatched the previous fall (see Fig. 5).

LABORATORY STUDIES

Respiration — Bottom samples were dredged from Char Lake, returned to the laboratory, and screened to remove mud. Larvae were then picked from trays with an Irwin loop or pipette, transferred to clean water, and placed in glass vials of 0.3, 2.6, or 3.2 ml capacity. The total time between collection and placement of animals in vials was 2–12 h, the larvae being kept between 0 and 4 C. Vials were filled with fresh lake water which had been aerated to remove excess gases, sealed with neoprene stoppers having a 26-gauge syringe needle inserted through the top, and placed in either an ice bath at 0 C or a water bath at 2 or 4 ± <0.1 C, in the dark. Control vials were filled along with experimental vials, using exactly the same procedure. *Lauterbornia* larvae live in tubes of cemented silt, and to test the effects of substrate on respiration, a small amount of oxidized bottom sediment was added to the control and experimental vials in several of the *Lauterbornia* experiments.

At the end of the experimental period (20–30 h), each vial was dried, unstoppered, and a water sample removed and injected into the 0.07-ml sample chamber of a Radiometer® blood-gas analyzer. The sample chamber was kept at 0 C in an ice bath. The gas analyzer was calibrated before and after a run with 0 C water of a known oxygen concentration, and the oxygen consumption of the experimental vial taken as the difference from the control vials, either from an in-line recorder, or from a digital reading on the instrument taken 3 min after sample injection. Larvae were subsequently identified to genus and instar, dried, and weighed.

To obtain the energy respired by a chironomid during its life, I used an oxycaloric coefficient of 3.6 kcal/g O_2 (Winberg 1971), and applied the appropriate respiration–weight relationship to the growth curves (see Results).

Calorific content — Larval dry weights were determined for freshly collected material, using aluminum foil pans dried at 55 C. Calorific determinations were made on a modified Gentry–Wiegert microbomb calorimeter (Welch 1973). Thirty-eight determinations on larvae (all but one on instars III or IV) gave 5.5 kcal/g ash-free dry weight. The average ash content, determined by ashing caloric samples at 550 C, was 10% except for *Heterotrissocladius*, which was 18%. I therefore used 5.0 kcal/g dry larval weight for all genera except *Heterotrissocladius*, for which I used 4.6 kcal/g dry weight. Values for weight, calories, and ash content of pupae, adults, and eggs are from Welch (1973). Larval growth is underestimated by some small, unknown amount because larval skin production was not measured. The pupal exuvium, much more robust than the larval skin, is 8% of the pupal weight, but less by energy content (Welch 1973).

Population energy flow — Ordinarily, population energy flow is computed from curves relating numbers with size, from which population growth, mortality, and respiration can be derived. In the absence of measurable mortality until April of the last year of growth, and because of the variability of year-class population estimates (see Fig. 15–19), the mean of the population estimates through April before emergence for each year-class has been applied against the growth and respiration curves. Mortality for April–July was calculated as:

$$\frac{[(\text{Mean no. through April}) - (\text{No. in July}]\ [(\text{Wt in July}) - (\text{Wt in April})]}{2}$$

and growth for the same period as:

$$\text{Mortality} + [\text{No. in July}]\ [(\text{Wt in July}) - (\text{Wt in April})]$$

Respiration for April–July uses the population mean between the two sampling times. This approach eliminates negative mortality estimates and results in smoothing the energy flow patterns, while the annual totals are the same as those calculated for each population estimate separately. A further advantage is that the 1970–71 energy flow can be calculated for *Pseudodiamesa*, *Orthocladius*, and *Lauterbornia*, even though they were not sampled in October 1970, January 1971, and April 1971, by using the means from other sampling periods.

Results

Life History

General — Char Lake chironomids pass 2 or 3 yr as larvae, emerging as adults during the short open-water period in mid-July to September. Mating usually takes place on the ice or at the shore edge, initiated by active males seeking passive females, but, during the infrequent calm periods, swarming also occurs, particularly by *Pseudodiamesa*. A few days are likely required for egg maturation between mating and egg-laying (Oliver 1968, and personal communication) although, when large numbers of newly emerged *Pseudodiamesa* are collected and enclosed in containers holding a dry substrate surrounded by water, a small fraction of the females will lay eggs within 24 h. *Lauterbornia* sp. is parthenogenetic, and nearly all females collected after emergence and placed in a calm location with water will soon lay their eggs. The wind blows most of the time at Resolute (mean annual wind speed 18.7 km h^{-1}), and, whenever calm weather occurs, the entire surface of the lake is covered with egg-laying adults within minutes. The eggs sink after oviposition. The pattern of egg deposition around the lake can be highly variable from year to year depending on wind direction and position of the ice cover, particularly for *Pseudodiamesa* which emerges early. *Pseudodiamesa* eggs held at 2.0 C hatched in 27 days; hatching for other species was similar, but hatching times were not determined exactly.

The newly hatched larvae of all species observed in the laboratory were planktonic and extremely active for a few hours after hatching, but quickly settled to the substrate. During extensive zooplankton sampling including night series (Rigler et al. 1974), we found only one or two larvae, within a meter of the bottom, and any planktonic existence of first-instar larvae must, therefore, be very short.

The duration of the pupal stage is about 14 days for all species. There were no detectable differences in larval growth rates between shallow (<4 m) and deep (5–25 m) water for each species. Growth is continuous throughout the year with no indication of suspended development over the winter, with the possible exception of *Orthocladius* (see below).

Larvae of all species feed on a mixture of surface algae (largely diatoms) and detritus, preferentially selecting organic over inorganic matter (Davies 1974). *Pseudodiamesa* larvae will readily eat other larvae when confined with them, but we never found larval remains in *Pseudodiamesa* fresh from the lake (Davies 1974; M. N. Charlton personal communication).

Potential predators are few. Unidentified water mites are moderately abundant in the moss zone and one to three larval mites are often attached to the thorax of emerged *Lauterbornia*,

TABLE 3. Head capsule depth in microns of Char Lake chironomid larvae, and percent increase (in parentheses) over preceding instar. Original measurements ±9 μ; 25 or more measured in each instar and species.

Genus	Instar I	II	III	IV	Mean increase (%)
Pseudodiamesa	127	218 (72)	346 (59)	528 (53)	61
Lauterbornia	73	105 (44)	191 (82)	309 (62)	63
Heterotrissocladius	64	100 (56)	173 (73)	273 (58)	62
Trissocladius	64	100 (56)	155 (55)	255 (65)	59
Orthocladius	64	105 (64)	164 (56)	273 (66)	62
Mean increase %		(58)	(65)	(61)	61

and occasionally *Paracladius*. These mites are engorged (D. R. Oliver personal communication) and transfer to the egg mass as soon as it is laid, but do not appear to feed on the eggs or larvae. The attachment to emerging females may serve largely as a dispersal mechanism. Benthic nematodes are abundant and include carnivorous forms. Parasitic nematodes were observed a few times inside larvae but the incidence was very low. Several times during the study, many-stalked colonial protozoa were seen attached to the head capsules of *Lauterbornia*, and less commonly to *Pseudodiamesa*, with no obviously deleterious effects. Arctic char (*Salvelinus alpinus*) are by far the most important predators on chironomids (see Discussion).

These chironomids pass through four instars, I–IV. Mature fourth-instar larvae that will be emerging within a few weeks, develop fat bodies and wing pads several weeks before pupation, when they are called prepupae. I distinguished instars on the basis of head capsule depth because this parameter is easily measured when the animal is curled and lying sideways, alive or dead. For all but *Lauterbornia*, the normal distribution of head capsule depths about the mean are nonoverlapping between instars, and, excluding *Paracladius* for which I had few measurements, there is an increase in head capsule depth of about 61% at each molt (Table 3). Third- and fourth-instar *Lauterbornia* exhibited a very broad, slightly overlapping range of head measurements. Since the species is parthenogenetic, the population consists of a series of clones, and any change in genes controlling larval shape will, therefore, be passed directly to the offspring, resulting in gradual broadening of characters within the population.

Specific — The monthly instar distributions of all larvae measured during the study are shown by year in Fig. 3; data for months with fewer than 10 larvae are excluded. Comparison of the 3 yr in Fig. 3 shows that, despite fluctuating numbers of larvae in successive year-classes, combining the data for the 3 yr into one composite year (Fig. 4) gives essentially the same instar changes throughout the year, and facilitates the task of tracing life histories. By looking at October–November for a given genus and following the instar distribution vertically with time, the growth of a year-class can be traced from birth to emergence. I have compiled the following life-history summaries (Fig. 5), based upon my interpretation of Fig. 3 and 4.

Trissocladius larvae hatch in late September and by November are passing into instar II. By late January (4 mo) nearly all are II. These molt to III starting July (10 mo) and by August (11 mo) most are III. They remain in III until the following April (19 mo), at which time they molt to IV. Peak emergence is early to mid-August (23 mo). The generation time is 2 yr, and at all times there are two year-classes present.

Pseudodiamesa also live 2 yr but grow more quickly. Larvae hatch in August and pass rapidly to II by October. Growth continues to be rapid and all are III by March (7 mo); III molt to IV in July–August (12 mo) and pass the winter as IV. Emergence is in mid- to late July (23 mo). Two year-classes are always present.

Lauterbornia sp. live 2 yr and are parthenogenetic. They hatch in September, grow rapidly, and all are II by February (5 mo). They pass to III in April–May (8 mo) and molt to IV from August (11 mo) onward. Two year-classes are always present.

Heterotrissocladius hatch about the same time as the other species but take 3 yr to mature. Larvae molt to II in December–January (4 mo) and remain as II until late summer. They then pass their second year as III, molting to IV late in the second summer (24 mo). Emergence is in late July of the third summer. At any time, three year-classes are present.

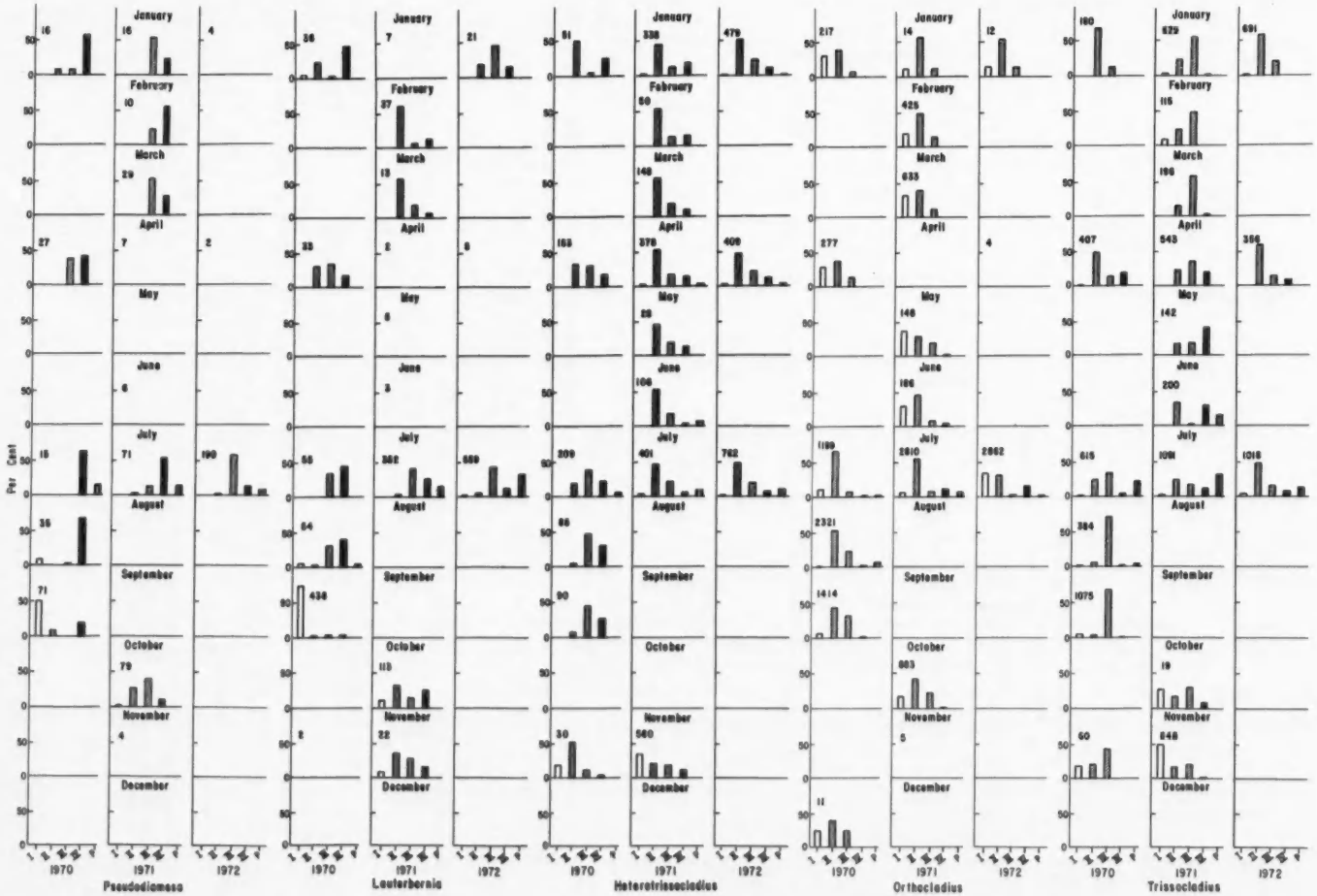

FIG. 3. Monthly instar distribution for chironomids taken during 1969–72 in Char Lake. Total number of specimens for each month in left corner. P = prepupae and pupae.

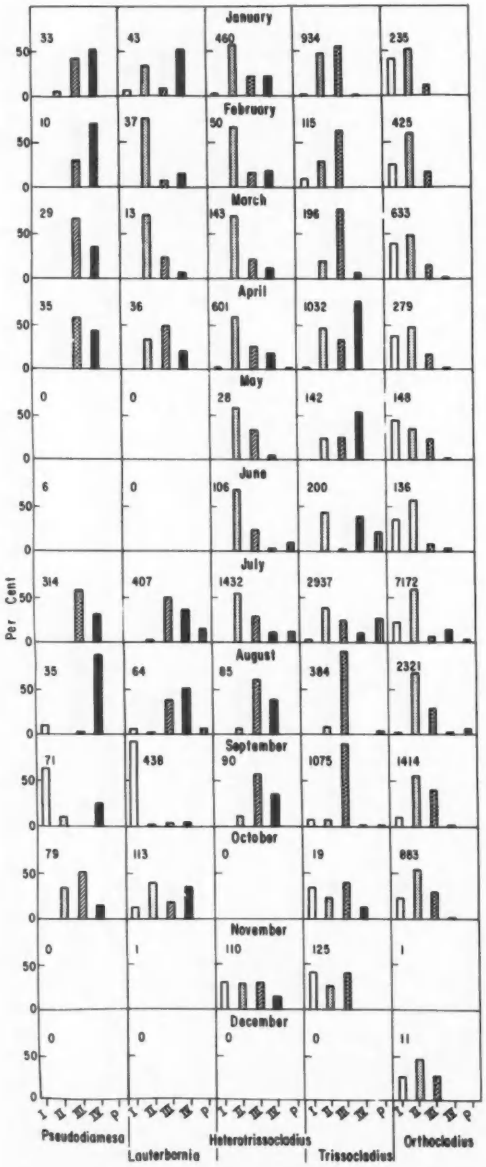

FIG. 4. Monthly instar distribution for chironomids taken during 1969–72 in Char Lake, showing the data in Fig. 3 combined into 1 composite yr. Total number of specimens for each month in left corner. P = prepupae and pupae.

Orthocladius also has a 3-yr cycle. The larvae hatch in late September but remain as I until the following summer, abruptly molting to II in July

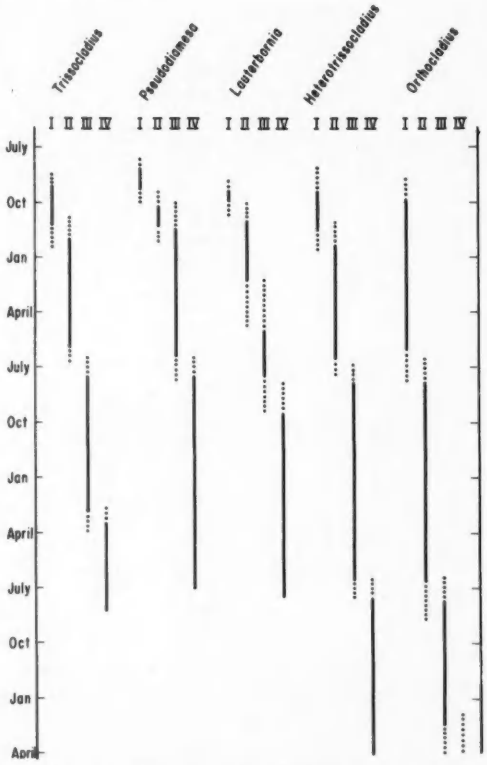

FIG. 5. Life-history summary of Char Lake chironomids showing instar changes with time.

(10 mo). They remain as II until the next July–August (22 mo), when they molt to III. They go to IV in spring, and emerge in mid-August of the third year.

There were too few *Paracladius* collected to warrant separate analysis. Instars I and II were present early in the summer, suggesting a 3-yr life cycle similar to that of *Orthocladius* or *Heterotrissocladius*. Because the two animals are about the same size, I used *Heterotrissocladius*' vital parameters for the few *Paracladius* larvae taken in quantitative sampling.

The growth curves for each genus are given in FIG. 6. *Lauterbornia* and *Pseudodiamesa* growth is rapid early in larval life and tapers off gradually before emergence, whereas *Trissocladius* continues to grow rapidly right up until emergence. *Heterotrissocladius* grows rapidly the first 2 yr, but very little during the third year after molting to instar IV. *Orthocladius* grows quite differently, with relatively slow growth in its second year but rapid growth the third year (see also Discussion).

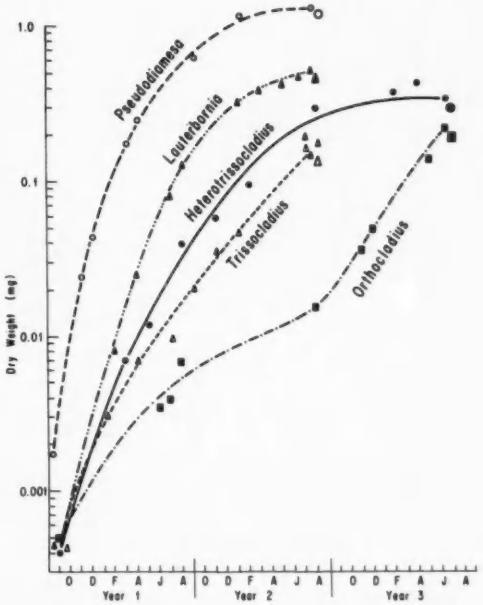

FIG. 6. Larval chironomid growth in Char Lake. Last point on each curve is the pupal weight.

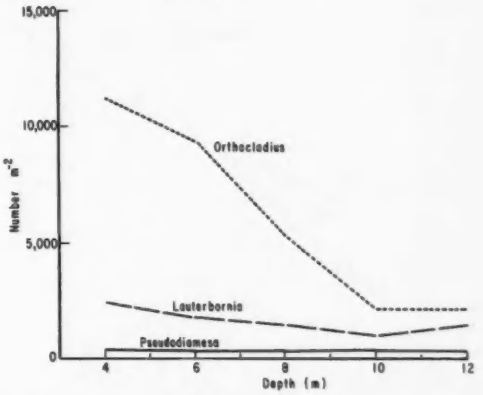

FIG. 7. Larval distribution in the moss zone, mean of four sampling periods, October 1971–July 1972.

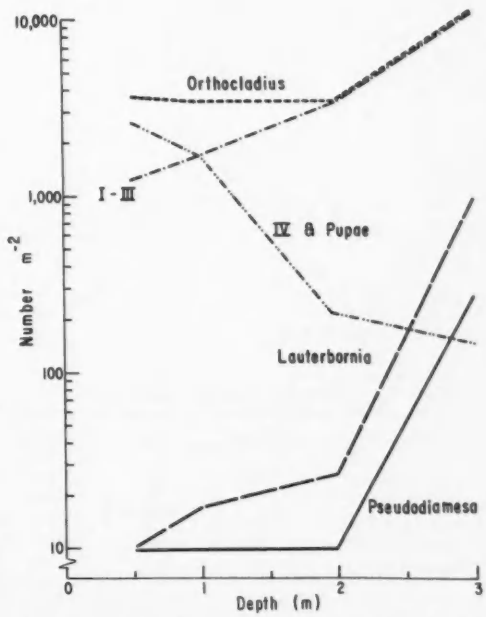

FIG. 8. Larval distribution in the rocky zone, July 1971, transect A.

LARVAL POPULATIONS

Depth distribution — In the sediment zone there was no consistent correlation of larval numbers with depth either by stage or total number. About 95% of the larvae occurring in the sediment zone where *Heterotrissocladius* or *Trissocladius*, and regressions on depth for these two species, by instar and life stage for each of nine sampling periods, showed no correlation significant at $P = 0.05$.

Within the moss zone, *Orthocladius* was negatively correlated with depth (Fig. 7), with an average density at 4 m 5 times that at 12 m. *Lauterborniella* was not strongly correlated with depth, and *Pseudodiamesa* numbers were very constant in the moss zone, ranging from 410 to 334 m^{-2} with no depth correlation.

In the rocky zone, *Pseudodiamesa* were nearly as abundant at 3 m as at 4 m in moss (Fig. 8) but were almost nonexistent above 2 m. *Lauterborniella* were also abundant at 3 m, dropping off sharply in shallower water. *Orthocladius* at first appears to have a more even distribution in the rocky zone than in the moss zone. There is a strong depth differentiation by stage in this species, however, as shown by Fig. 8 for transect A in 1970 and 1971. The first three stages fell off exponentially toward shallow water while the last three stages, those that were to emerge shortly, increased exponentially toward shallow water. Breakdown by instar (Fig. 9) shows that I and II were concentrated at 2–3 m, III was more evenly distributed, and mature larvae and pupae were an order of magnitude more abundant at 0.5 m than at 3 m. I believe that early instars remain below 2 m and are not frozen

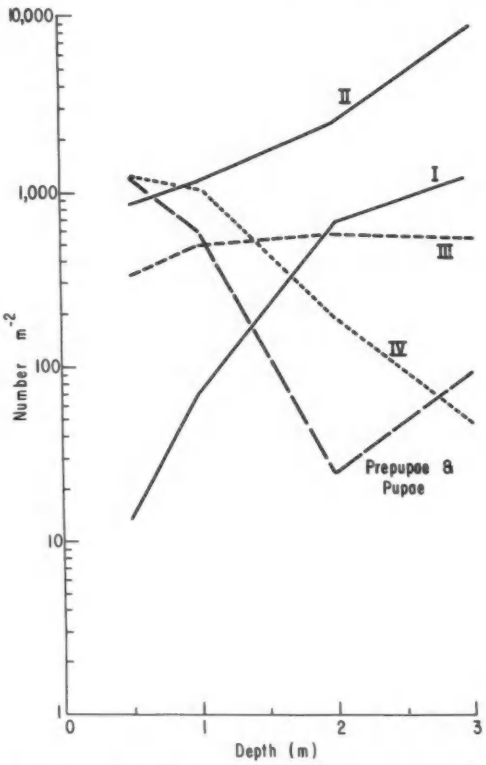

FIG. 9. *Orthocladius* distribution in the rocky zone, July 1971, transect A, by instar.

TABLE 4. Percent larvae in each zone, July 1971.

Genus	Rocky	Moss	Sediment
Pseudodiamesa	42	46	12
Lauterbornia	58	33	9
Heterotrissocladius	1	0	99
Trissocladius	4	0	96
Orthocladius	55	43	2

overwinter, while fourth instar migrate into shallow water beneath the ice when the ice-sediment interface melts in June. Relatively few larvae of the three species, therefore, remain in the rocky zone during freezeup.

Among the three zones, 96% of the *Trissocladius* and 99% of the *Heterotrissocladius* larvae (Table 4) occurred in the sediment in July 1971, the only time when the three zones were sampled simultaneously. The other three species were more evenly divided between the rocky and moss zones, with few living in the sediment zone.

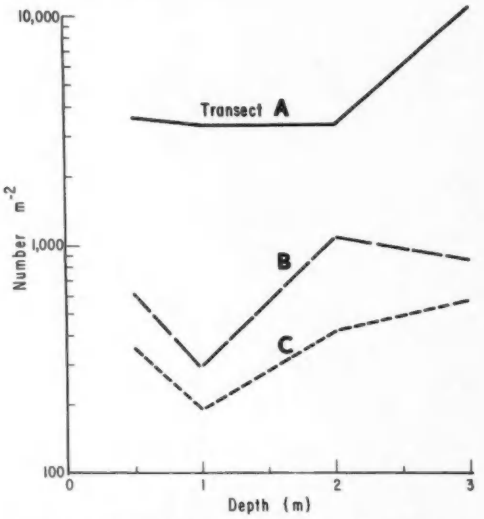

FIG. 10. *Orthocladius* distribution in the rocky zone, all stages combined, transects A, B, and C 1971.

For some reason, possibly because a different person took the samples, the July 1971 moss figures were low compared with the next four sampling periods, so the proportions of *Pseudodiamesa*, *Lauterbornia*, and *Heterotrissocladius* occurring in the moss zone were probably higher than indicated by Table 4.

Horizontal distribution — The July 1972 sediment core series showed no significant differences in larval abundance within the sediment zone. A few cores taken in the southwest corner were lower in total numbers than the zone-wide mean, but these cores were shallow (12–15 m), contained abundant moss fragments, and therefore were not comparable with deeper cores. The emergence data (Welch 1973) from four transects around the lake also showed that *Trissocladius* and *Heterotrissocladius* were evenly distributed in the sediment zone.

In the moss zone there were no great differences in larval numbers between the three areas sampled in July 1972, except that *Orthocladius* was half as abundant at station E as at A and D. Emergence data also showed no marked differences around the lake (Welch 1973), so the July 1971–April 1972 moss zone data, from transect A only, were used unaltered.

In the rocky zone the three areas sampled in 1971 did vary, with populations much higher at transect A than at B and C (e.g. Fig. 10 for *Orthocladius*). The 1970 cake-pan data from

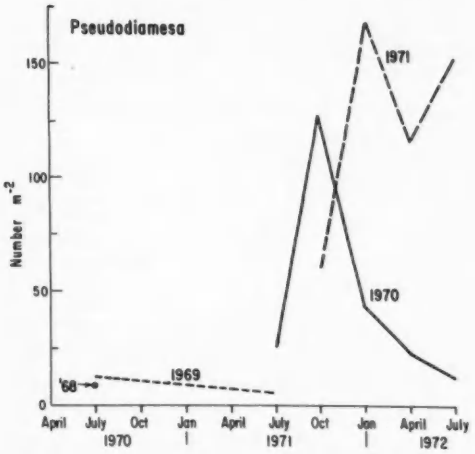

FIG. 11. *Pseudodiamesa* year-class strength, No. m^{-2}. There is a separate estimate for each specified year-class at each 3-mo sampling time in Fig. 11–15.

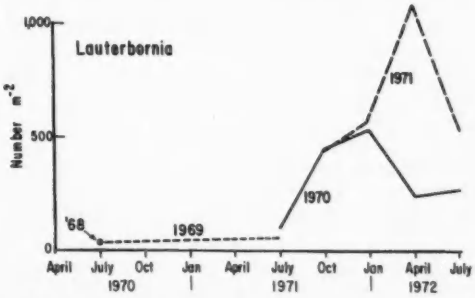

FIG. 12. *Lauterbornia* year-class strength, No. m^{-2}.

transect A were adjusted downward by the 1971 ratio $\frac{A+B+C}{A}$.

Abundance — Figures 11–15 show the population of each year-class with time. The July 1971 population estimates for *Pseudodiamesa*, *Lauterbornia*, and *Orthocladius* were very low because the moss zone figures were probably low on that date. Nonetheless, there were clear-cut trends.

First, there was a general increase in year-class strength with time, shown more clearly by Fig. 16. The 1967 figure includes only one estimate for *Orthocladius* and two estimates for *Heterotrissocladius* and are probably low compared with the 1968–71 figures, which include all five species and more population estimates for each year-class. The average increase was 5 times for

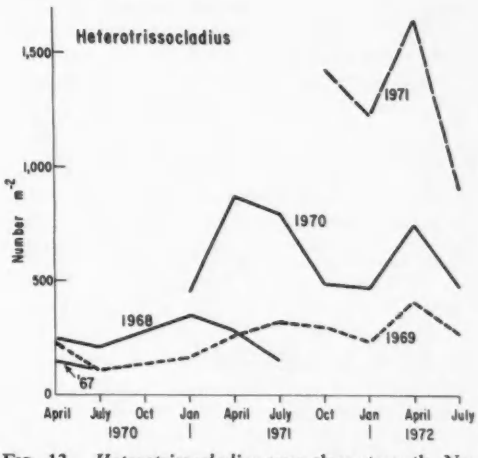

FIG. 13. *Heterotrissocladius* year-class strength, No. m^{-2}.

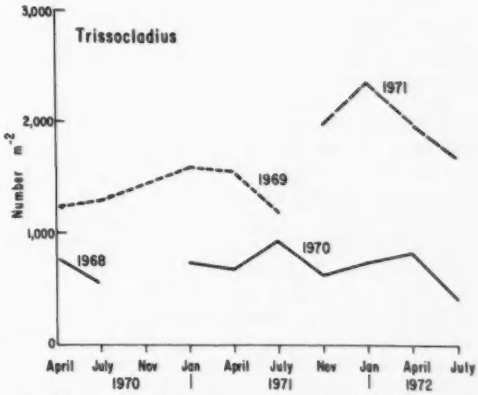

FIG. 14. *Trissocladius* year-class strength, No. m^{-2}.

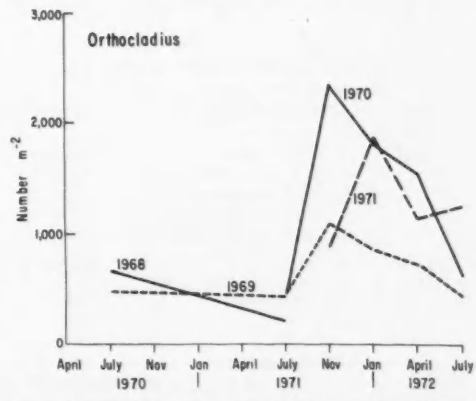

FIG. 15. *Orthocladius* year-class strength, No. m^{-2}.

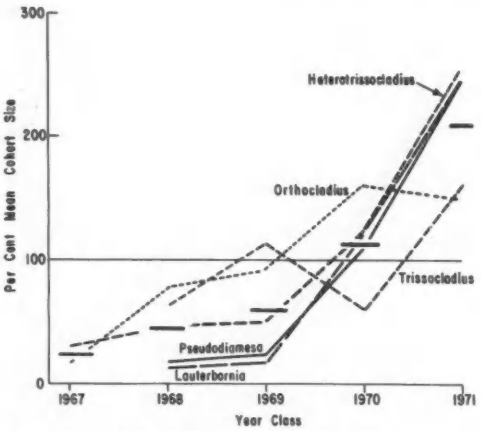

FIG. 16. Relative year-class strength 1967–71. Mean for each year indicated by horizontal bar.

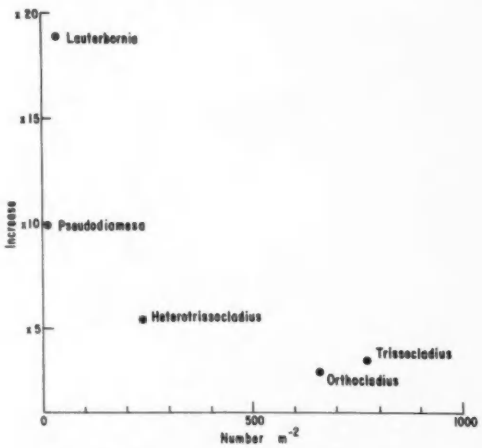

FIG. 17. Percent increase in year-class strength between 1968 and 1971, vs. number in the 1968 year-class.

1968–71. The increase was not the same for all species; rather, the least abundant species increased the most (Fig. 17).

Second, there was little change in the size of a year-class except for the last few months of larval life (Fig. 11–15). The overall trend is more clearly shown in Fig. 18, where I have plotted a three-point moving average of all the year-class estimates shown in Fig. 11–15 against the same relative time scale of birth to pupation. The apparent negative mortality early in larval life cannot be real, and is probably an artifact of the sampling program. There were few first-instar larvae in the samples checked for picking efficiency; there was likely greater handling loss of such larvae from the fall samples, while the larger larvae were probably sampled more accurately. Mortality cannot be zero, but is un-

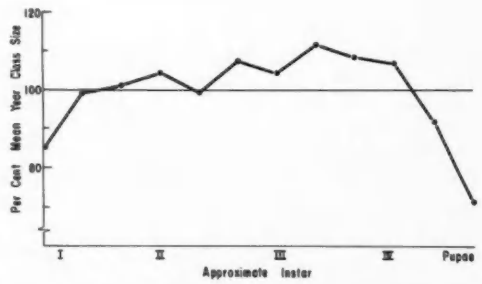

FIG. 18. Relative numbers of larvae throughout larval growth from hatching to pupation, expressed as a percent of the mean number in each year-class, 3 pt. moving average for all species combined.

TABLE 5. Percent decrease in numbers of the maturing year-class between April and July.

Genus	Year-class	No. m^{-2} April	No. m^{-2} July	Mortality (%)
Pseudodiamesa	1970	23.0	12.5	46%
Lauterbornia	1970	243	274	−13%
Heterotrissocladius	1967	150	111	26%
"	1968	242	149	38%
"	1969	416	273	34%
Trissocladius	1968	786	557	29%
"	1969	1558	1190	24%
"	1970	813	404	50%
Orthocladius	1969	740	452	39%
	Mean reduction in numbers between April and July = 30%.			

TABLE 6. Potential and actual emergence, July 1971, where potential emergence is the estimate of mature larvae present in early July at the time of quantitative sampling, and actual emergence is from subsequent trap catches (Welch 1973).

Genus	Potential emergence no. m^{-2}	Actual emergence no. m^{-2}	Percent emerging
Pseudodiamesa	6.0	20.6	343
Lauterbornia	56.8	14.6	26
Heterotrissocladius	149.2	9.1[a]	6[a]
Trissocladius	1190.3	367.0	31
Orthocladius	219.6	275.0	125
Sum (without *Heterotrissocladius*)	1472.7	677.2	46

[a]Most of the *Heterotrissocladius* emergence was not measured (Welch 1973).

doubtedly very low throughout most of the larval life.

Between April and July of the last year of larval life, mortality was relatively heavy, averaging 28% for the nine year-classes (Table 5), or 34% without *Lauterbornia*, whose apparent negative mortality could be a result of partially incorrect differentiation between the 1970 and 1971 year-class in April 1972 (see Fig. 3 and 4).

Mortality of mature larvae and pupae was also high in summer, about 50%, as shown by a comparison of mature larvae sampled quantitatively in early July with numbers taken in emergence traps in late July and August 1971 (Table 6). Excluding *Heterotrissocladius*, whose emergence was not completely measured (Welch 1973), a mean of 46% of the mature July larvae were actually trapped as adults. This was equal to 53% of the potentially emerging biomass on a weight basis.

I conclude that with a 30% reduction in numbers between April and July 1971, and a loss of 50% from then to emergence, about 35% of the chironomids maturing in April succeeded in emerging in July–August.

RESPIRATION

The results of a polynomial fit to the log respiration–log weight data at 0 C are given in Table 7. The linear fit gave a good approximation for all genera, with a mean slope of 0.79. In three of the five genera, a third or fourth order polynomial gave a significantly better fit ($P = 0.01$, Table 7); however, for *Pseudodiamesa*, much of the variability about the linear relationship results from several scattered points at very low weights, and I think for this species the linear relationship gives the most realistic fit.

The relationships for the different species were compared by grouping the data into relatively narrow weight ranges and applying a two-way analysis of variance. The results showed that the relationships for *Trissocladius* and *Orthocladius* were not significantly different from each other (P between 0.01 and 0.05). All other intergeneric

TABLE 7. Respiration–weight relationships for Char Lake larval Chironomidae at 0 C.[a]

	Number of Determinations	Order of best polynomial	Coefficients of linear fit $Y = A + BX$ (SE)	Coefficients of best polynomial
Pseudodiamesa	87	Fourth	A = −1.2272 (.065)[b]	A = −1.2724
			B = .6202 (.039)	B = .3368
				C = .0970
				D = .1304
				E = .0198
Lauterbornia	217	Third	A = − .8431 (.104)	A = −2.8994[b]
			B = 1.0277 (.036)	B = −1.7387
				C = − .8031
				D = − .0638
Heterotrissocladius	152	First	A = −1.9016 (.116)[b]	—
			B = .7360 (.041)	—
Trissocladius	221	First	A = −1.2417 (.137)[b]	—
			B = .7652 (.038)	—
Orthocladius	214	Third	A = .9322 (.191)	A = −3.3495[b]
			B = .7935 (.052)	B = −1.3421
				C = − .5471
				D = − .0411
			$\bar{B}$ = .7985	

[a]Where Y = ln (μg O_2 consumed/h); A = constant; B = ln (milligrams dry weight).
[b]Used to compute larval energy budgets.

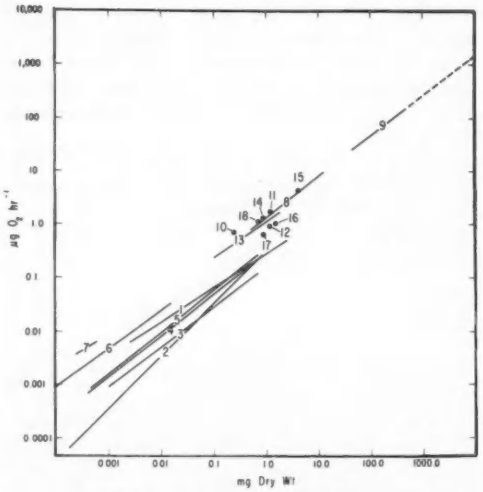

FIG. 19. Respiration–weight relationships for Chironomidae and other animals. Char Lake data: 1. *Pseudodiamesa*, 0 C; 2. *Lauterbornia*, 0 C; 3. *Heterotrissocladius*, 0 C; 4. *Trissocladius*, 0 C; 5. *Orthocladius*, 0 C; 6. *Limnocalanus macrurus*, 0 C; (Roff 1972); 7. *Cyclops vernalis*, 0 C; (Taube-Nauwerck 1972); 8. *Mysis relicta*, 0 C (Lasenby and Langford 1972); 9. *Salvelinus alpinus*, 2 C (Holeton 1973). Others: 10. *Chironomus anthracinus*, littoral zone, 13 C assuming dry:wet weight = 0.15 (Berg et al. 1962); 11. *C. anthracinus*, profundal zone (Berg et al. 1962); 12. *Procladius*, (Berg et al. 1962); 13. *Chironomus riparius*, 10 C, assuming dry:wet weight = 0.15 (Edwards 1958); 14. *Chironomus dorsalis*, 5 C, dry:wet weight = 0.15 (Konstantinov 1958); 15. *C. plumosus*, 2 C, dry:wet weight = 0.15 (Konstantinov 1958); 16. *Pseudodiamesa nivosa*, 2 C, dry:wet weight = 0.15 (Konstantinov 1958); 17. *Prodiamesa olivacea*, 2 C, dry:wet weight = 0.15 (Konstantinov 1958); 18. *C. dorsalis*, 0 C, dry:wet weight = 0.15 (Konstantinov 1958).

comparisons demonstrated highly significant differences ($P = 0.01$).

There were no significant correlations with time of year or vial size. There was a slight but insignificant decline in respiration rate with increasing experiment duration at 0 C. At 2 C there were highly significant ($P = 0.01$) decreases in respiration with longer experiment duration. I also found very high Q_{10}'s within this narrow temperature range, averaging about 12, which probably resulted from poor experimental design, since nearly all the 2 C experiments were of shorter duration than those at 0 C. I cannot, therefore, draw any firm conclusions as to the effect of temperature.

There was a significant ($P = 0.01$) decrease of 31% in respiration rate when substrate was present in *Lauterbornia* vials. While other genera lay quietly on the bottom of the vials, *Lauterbornia* actively swam for a number of hours before settling down. When sediment was present, *Lauterbornia* began building a tube almost immediately. The decrease in respiration when substrate is present is, therefore, probably due to a decrease in swimming activity. Furthermore, large *Lauterbornia* swim more actively than small ones, which may account for the relatively steep slope (1.03) in the log weight–log respiration for this genus (Fig. 19 and Table 7).

TABLE 8. Comparison of fourth-instar and pupal respiration rates.

Genus	Number of determinations		Pupal rate/ 4th-instar rate
	4th instar	Pupae	
Pseudodiamesa	57	15	.82
Lauterbornia	136	14	.43[a]
Heterotrissocladius	47	18	1.05
Trissocladius	97	39	.80

[a]Significant at $P = .01$.

For the four genera measured, three show decreased pupal respiration rates compared with the fourth-instar rate, with the difference for *Lauterbornia* significant at $P = 0.01$ (Table 8). Since pupae are much less mobile than larvae, it is probable that a decrease in swimming activity accounts for at least part of the difference, particularly in *Lauterbornia*. This is supported by the *Heterotrissocladius* results where the pupal and fourth-instar rates were comparable; *Heterotrissocladius* larvae were virtually immobile in the experimental vials.

ENERGY FLOW

Paracladius — In July 1971, 80% of the *Paracladius* larvae were found in the rocky zone, and 20% in the moss zone. Applying this ratio to the July 1970 rocky zone data and to the July 1972 moss zone data gave nine population estimates distributed over the 1967–71 year-classes. There was a mean of 16.5 m^{-2} individuals in each year-class or about 50 larvae m^{-2} at any one time, which was less than 1% of the chironomid total. *Paracladius* respiration was 72, 24, and 13 calories m^{-2} in 1970, 1971, and 1972, respectively, less than 1% of total chironomid respiration. Emerging *Paracladius* biomass was 1% of the total in 1971 (Welch 1973). Because of the low numbers sampled and because its energy flow is less than 1% of the total, I have

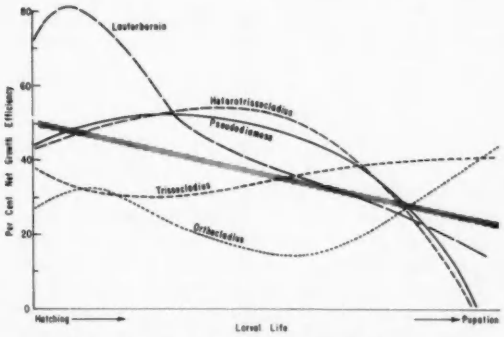

FIG. 20. Net growth efficiency of larvae from hatching to pupation. Heavy hatched line is the mean for all groups.

TABLE 9. Growth, respiration, and net growth efficiency for a single larva from hatching to pupation.

Genus	Respiration (*calories*)	Growth (*calories*)	NGE $\left(\frac{G}{G+R}\right)$
Pseudodiamesa	12.052	6.639	.355
Lauterbornia	6.562	2.554	.280
Heterotrissocladius	3.133	1.737	.357
Trissocladius	1.175	.730	.383
Orthocladius	1.893	1.104	.368
Mean			.349

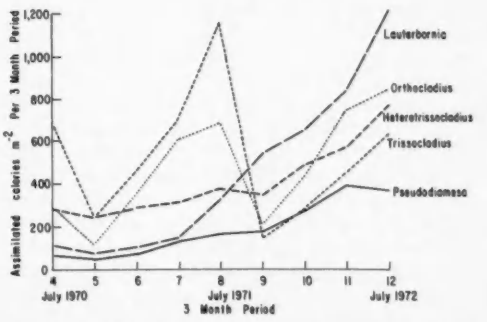

FIG. 21. Assimilated energy (growth and respiration) per 3-mo period for each genus.

excluded *Paracladius* from further discussion of chironomid energy flow.

Larval — Net growth efficiency (NGE) for each species appeared to change considerably during larval life (Fig. 20), but since NGE was derived from curves fitted to respiration and growth, much of the apparent variation is probably not real. Also, the early high NGE for

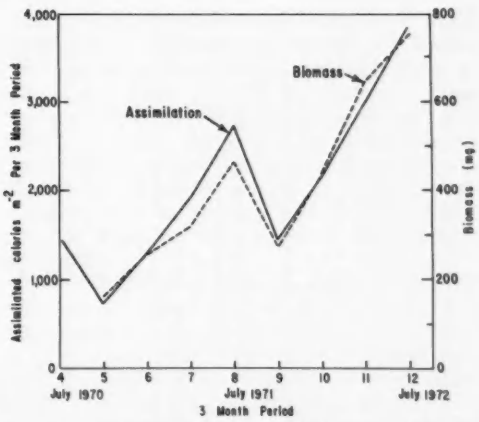

FIG. 22. Assimilated energy and biomass, all Char Lake Chironomidae together, per 3-mo period.

Lauterbornia probably resulted from an artificially high respiration rate for large larvae, skewing the lower end of the weight–respiration regression downward. For the five genera combined, there was a clear downward trend in NGE, which dropped from about 50% early in life to 25% at pupation. Without *Lauterbornia* the remaining four genera had a mean NGE decreasing gradually from 40 to 30% with increasing larval age. The mean NGE for an individual larva from egg to pupa was remarkably similar for all genera, averaging 35% (Table 9).

Population — Energy flow by genus (Fig. 21) shows that *Trissocladius* and *Orthocladius*, which have very rapid growth the last few months of larval life (Fig. 6), varied up to 10 times in trimonthly energy flow in a given year, whereas species with less rapid growth their last spring (*Heterotrissocladius*, *Pseudodiamesa*, and *Lauterbornia*) fluctuated much less within the year. There was a general increase in energy flow throughout the study period, corresponding to the population increases. *Lauterbornia* made a particularly large gain, its trimonthly energy flow going from next to lowest at .11 kcal m^{-2} in July 1970 to highest at 1.2 kcal m^{-2} in July 1972. At the same time, *Trissocladius* went from highest to second lowest, although the net change was slight. Because of the relative importance of *Trissocladius* and *Orthocladius*, total chironomid energy flow was also strongly seasonal, with a gradual increase from fall to the following summer, and a sharp drop after emergence (Fig. 22). Total chironomid biomass (B) ranged from 0.15 to 0.75 g dry weight m^{-2} and closely paralleled energy flow (Fig. 22). Equating growth (G) to

TABLE 10. Population energy flow for Char Lake Chironomidae in calories m^{-2} lake surface.

Genus	For all year-classes present: No. m^{-2}	Mean biomass dry wt mg	Mean biomass (B) calories	G	R	P:B	Net growth efficiency $\frac{G}{G+R}$	For the maturing year-class: Apr.–July mortality	July to emergence mortality	Emergence	Total production[c]
Fall 1970 to Summer 1971											
Pseudodiamesa	68	23	116	177	244	1.5	.42	45	−100	140	85
Lauterbornia	378	26	129	241	428	1.9	.36	0.0	82	35	117
Heterotrissocladius	1098	114	525	444	786	.8	.36	147	224[a]	15[a]	386
Trissocladius	2121	102	510	995	1578	1.9	.39	129	588	284	1001
Orthocladius	2582	53	267	626	1182	2.3	.35	364	76	319	759
Sum	6247	318	1547	2483	4218	1.6	.37	685	870	793	2348
Fall 1971 to Summer 1972									July standing biomass[b]		
Pseudodiamesa	176	99	494	499	726	1.0	.41	296	83		379
Lauterbornia	1037	133	664	990	2264	1.5	.30	139	699		838
Heterotrissocladius	2182	185	851	914	1270	1.1	.42	0.0	413		413
Trissocladius	2696	54	272	564	962	2.1	.37	199	296		495
Orthocladius	3324	77	586	796	1439	1.4	.36	269	499		768
Sum	9415	548	2867	3763	6661	1.3	.36	903	1990		2893

[a]Emergence underestimated, resulting in overestimation of July-emergence mortality for *Heterotrissocladius*.
[b]For 1970–71, the July biomass is divided into July to emergence mortality and emergence.
[c]The sum of mortality and emergence is the energy passed on to the next trophic level. In the long term it is equal to growth for all year-classes. During these 2 yr it averages less than growth because the populations were expanding.

production (P), P:B was 1.6 and 1.3 for the 2 yr (Table 10).

Discussion

Life History

Since all energetics calculations hinge on the correct interpretation of the duration of different generations, further discussion of the life-history interpretations given in the Results section is in order. Could, for example, one or more genera be inactive or in diapause over winter? Only *Orthocladius* has a winter instar distribution pattern stable enough to suggest diapause (Fig. 5), and molting appears to take place largely in June, July, and August, when instar I go to II and II go to III. However, third instar molt to IV about March, and no indication of diapause or inactivity was noted in *Orthocladius* larvae which were collected live throughout winter for respiration measurements. It is possible that most growth takes place in the summer, but I could not detect this because there were few times in the year that *Orthocladius* year-classes could be separated for weight measurements, so the smooth *Orthocladius* growth curve (Fig. 6) was drawn accordingly.

Another possibility is that generation times are different from those proposed. It is highly unlikely that *Lauterbornia*, *Heterotrissocladius*, *Trissocladius*, or *Orthocladius* have 1-yr life cycles, given the high percent of second instar present at least until early spring, which precludes emergence the same year. *Pseudodiamesa* are entirely III and IV by February, but considering that *Pseudodiamesa* emergence is completed by early August (Welch 1973), the III and IV present in July and August could not emerge until the following year. Only if there were a mixture of 1- and 2-yr life cycles within a given genus could there be larvae emerging after 1 yr. There is no indication that this is so, but the possibility cannot be disproven by the available data. The same thing applies to a mixture of 2- and 3-yr cycles within the same genus — it appears improbably but it cannot be disproven. Given the highly synchronized nature of the *Heterotrissocladius* molt from second to third instar and the synchronized *Orthocladius* molt from first to second instar (Fig. 4), it seems to me very improbable that a significant portion of either of these 3-yr genera are completing their larval growth in 2 yr. *Orthocladius* is represented in Char Lake by two species, one confined largely to the moss zone, the other to the rocky zone, and a division of the *Orthocladius* instar data from Fig. 4 according to the rocky and moss zones for the 3 yr showed no differences in instar distribution, again indicating that the two species have similar generation times and molt patterns. One final piece of evidence indicating that *Heterotrissocladius* and *Orthocladius* are not completing their life cycle in 2 yr is the fact that, if respiration is worked out on the basis of a 2 instead of 3-yr cycle, the resultant net growth efficiency is on the order of 50% or more, which is quite different from the other three genera (Table 9).

When all the year-classes for which I have data were being formed, 1967–71, the ice left Char Lake between July 25 and August 18, whereas in 1972, open water reached a maximum of only 16% in August. Could such years delay chironomid life cycles by a year? For *Heterotrissocladius*, which attempted to emerge in normal numbers beneath the ice in 1972 (Welch 1973), the life cycle was not delayed, whereas for *Orthocladius*, which attempted to emerge in very low numbers only (Welch 1973), most of the emerging 1969 year-class apparently overwintered in 1972–73, perhaps as prepupal larvae. This is the only evidence I have for altered generation times, and it did not apply to the study period. I never found prepupal larvae in fall that had failed to emerge. The very small year-class of *Heterotrissocladius* and *Trissocladius* which resulted from the 1972 summer ice conditions could be followed to 1973 and 1975 and further corroborated the life-history interpretations for those two genera (see discussion below).

Physiology

Physiologically, these high latitude chironomids do not seem to differ from low latitude larvae. A linear fit to the log weight–log respiration data gave an overall weight exponent of 0.79 (Table 7), which conforms to the many determinations made on low latitude animals. Oxygen consumption is no greater than in temperate region chironomids (Fig. 19), and I conclude, as did Holeton (1973) and Lasenby and Langford (1972), that Char Lake animals do not show any metabolic compensation as suggested by Scholander et al. (1953) and others. The average net growth efficiency of 30–40% is also average for freshwater invertebrates (Welch 1968). Calorific values are similar to those for Marion Lake, British Columbia, larvae (McCauley and Tsumura 1974). There is no evidence of diapause or suspended development, despite ambient temperatures close to 0 C, although Char Lake chironomids survived in the laboratory at temperatures over 15 C. Thus, while these animals at latitude 75°N are living near

one extreme of a range of environmental variables, their metabolic response is not extraordinary aside from a lowering of the minimum temperature for normal activity.

Energy Flow

The mortality of mature larvae and pupae is due to char predation (personal observation). Char stomachs are virtually empty until spring; the fish are sluggish and do not take artificial bait readily until May, and their stomachs are not full until June. In July and August all larger char stomachs are packed with mature larvae and pupae; during this narrow time period, char may be taking a constant quantity of prey each year. After the termination of emergence and the onset of snow, ice, and rapidly decreasing light levels in mid-September, the char once again have little in their stomachs. Maximum production of each chironomid year-class occurs because the animals are cropped near or at the end of their growth period. If char ate no emerged adults they would still be taking 65% of chironomid production (Table 10), and their utilization of chironomid production is likely even higher since they do feed on adults to some extent.

Char ingest on the order of 2.7 kcal m^{-2} yr^{-1} (F. H. Rigler unpublished data). Total chironomid production was 2.3 and 2.9 kcal m^{-2} for the 2 yr studied. If emerged adults largely escaped predation, much less than 2.3 kcal m^{-2} chironomid flesh was consumed by char from August 1970 to July 1971, an early ice-out year. In 1972, most of the emerging adults were trapped beneath the ice where they were vulnerable to predation, and chironomid production alone could possibly have met char demands that year. Chironomid production is closely correlated with cohort size and occurs largely in the last year of life. The yearly production in Table 10 is primarily contributed by the 1968 and 1969 year-classes for 3-yr species and the 1969 and 1970 year-classes for 2-yr species. Figure 16 shows that these year-classes constitute an average for the five year-classes studied. I tentatively conclude, therefore, that, on the long term, chironomid production provides most but not all the energy ingested by char, and that about 75% of the chironomid production goes to char.

Comparing Char Lake zooplankton with chironomids, *Limnocalanus macrurus* alone assimilate 10.5 kcal m^{-2} yr^{-1}, or about 80% of total zooplankton energy flow (F. H. Rigler unpublished data), compared with chironomid assimilation at 8.6 kcal m^{-2} yr^{-1}. But *Limnocalanus* production was much lower, 0.13 kcal m^{-2} against 2.6 kcal m^{-2} for chironomids, because of a low overall population net growth efficiency of 13.7% (Rigler et al. 1974). Net growth efficiency of stages nauplius (N) IV to copepodite (C) V averaged 35%, the same as the chironomid mean, but long-lived adult *Limnocalanus* accounted for most of the population respiration. The mortality of *Limnocalanus* from N I to C VI was only 59% (Rigler et al. 1974), similar to the 65% mortality from first instar to adult for chironomids, and was clearly density-dependent (Fig. 23). *Limnocalanus* populations varied about 2 times from 1969 to 1972, compared with 5 times variation for chironomids between 1968 and 1971.

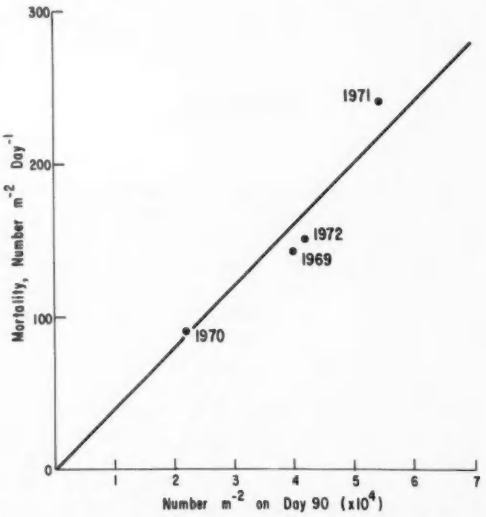

FIG. 23. Daily mortality of four *Limnocalanus macrurus* year-classes plotted against total numbers m^{-2} on day 90 (from regressions given by Rigler et al. 1974).

There is little chironomid energy flow data for other lakes, which limits comparisons. Absolute energy flow is of course many times lower

TABLE 11. Chironomid energy flow compared with photosynthesis in kilocalories m^{-2} yr^{-1}.

G	G + R	Photosynthesis	$\frac{G}{\text{Photo}}$ (%)	$\frac{G+R}{\text{Photo}}$ (%)
		Char Lake		
3.12	8.6	209	1.5	4.1
		Lake Esrom		
150.6	512.4	2440	6.1	21.0
		Lago Pond		
326.2	409	7389	4.4	5.5

TABLE 12. Adjusted annual P:B ratios for Char Lake Chironomidae according to generation time, using mean annual production and biomass from Table 10.

Genus	Mean annual production (*calories*)	Mean annual biomass (*calories*)	P:B	P:B × generation time (*yr*)
Pseudodiamesa	338	305	1.1	2.2
Lauterbornia	615	396	1.6	3.1
Trissocladius	779	391	2.0	4.0
Sum of 2-yr genera	1732	1092	1.6	3.2
Heterotrissocladius	679	688	1.0	3.0
Orthocladius	711	476	1.7	5.0
Sum of 3-yr genera	1390	1164	1.2	3.7

through Char Lake chironomids compared with productive temperate systems (Table 11). As a percentage of total plant production, however, it is more similar to values from Lake Esrom, a eutrophic Danish lake (Jónasson 1972) and Lago Pond, a fertilized Georgia farm pond (Welch 1967). Still, a smaller proportion of primary production is assimilated by chironomids in Char Lake than by those in Lake Esrom. A comparison of total benthic invertebrate energy flow would reduce this discrepancy because chironomid production in Char Lake is probably less than half that of the total benthos (Rigler unpublished data), whereas in Lake Esrom, chironomid production is about 85% of the total.

The annual P:B ratios, or turnover rates, for Char Lake chironomids are of course low (Table 10). Waters (1969) demonstrated theoretically that freshwater invertebrate turnover rates per generation should normally range from 2.5 to 5.0, with a mode about 3.5, just as is found in actual populations. Johnson (1974) pointed out that if the annual P:B ratios for non-univoltine species are multiplied by the generation times in years, the resultant ratios are similar to those for annual species. This is corroborated by the data for Char Lake chironomids (Table 12). Combining both years for each genus from Table 10 to arrive at a mean annual turnover rate, the 2-yr chironomids have an annual P:B of 1.6, or 3.2 when multiplied by the generation time; the corresponding figures for the 3-yr genera are 1.2 and 3.7. The mean of 3.2 and 3.7 is about 3.5, as predicted by Johnson. This result suggests that standing crop and generation times can be used to approximate annual production for arctic freshwater invertebrates as well as for temperate region animals.

POPULATION CONTROLS

There was no detectable mortality until the last year of larval life, indicating that predators, disease, and parasites do not greatly affect early instars. Mortality of the maturing year-class averaged 30% between April and July with no correlation between percent mortality and numbers of larvae in April (Table 5). The absolute number of larvae removed from each year-class during this spring period, presumably by char, was proportional to the numbers present. There were insufficient data (1971 only) for the period, July to emergence, to decide whether a constant amount, or a constant proportion, of chironomids were removed at that time each year.

The most important control on Char Lake chironomid populations is probably the summer environmental conditions for emergence and egg laying. To test this hypothesis, I sampled the sediment zone for *Heterotrissocladius* and *Trissocladius*, taking 18 cores at 16.0 m on July 18, 1973, and 20 cores at 19.0 m on July 10, 1975. For *Trissocladius*, all the 51 larvae (674 m^{-2} of lake surface) found in 1973 were prepupal instar IV belonging to the 1971 year-class with no members of the 1972 year-class present. In 1975 there were 1666 m^{-2} of the 1973 year-class, but only 190 m^{-2} 1974 year-class. For *Heterotrissocladius* in 1973, there were 305 m^{-2} 1970 year-class, 714 m^{-2} 1971 year-class, and 89 m^{-2} 1972 year-class; in 1975 there were 166 m^{-2} 1972 year-class, 562 m^{-2} 1973 year-class, and 940 m^{-2} 1974 year-class. 1971 was an early and mild year with ice-out on July 25, whereas 1972 was exceptionally cold and late. The ice did not leave the lake, and open water reached a maximum of 16% of the lake surface in mid-August 1972, and by then temperatures were so low that the ice sheet had solidly refrozen and emerging pupae could no longer make their way up through cracks in the candled ice surface (see also Welch 1973). Ice-out was August 10, 1973, at an unknown time in 1974, and on August 6, 1975.

I interpret these data as follows. *Heterotrissocladius* emerges early, in late July, and had some success in getting through the ice and laying eggs

in 1972, although the two estimates for the 1972 year-class, 89 m^{-2} and 166 m^{-2}, are much lower than for previous year-classes. The 1973 and 1974 year-classes were of average abundance. *Trissocladius* emerges later, in mid-August, could not penetrate the 1972 ice surface in large numbers, and the 1972 year-class was, therefore, virtually nonexistent. The 1973 year-class was normal, but the 1974 year-class was again extremely low despite favorable ice conditions because of the scarcity of parental (1972) stock. This information is consistent with the hypothesis that year-class strength is controlled by summer emergence and egg laying conditions, contributing to oscillations in abundance that could last at least two and possibly three generations, or 6–9 yr.

Potential egg production in 1971 was 49,000 m^{-2} (Welch 1973), from which an average year-class strength of 5,374 larvae m^{-2} were present during the next four sampling periods (Fig. 12–15). Since 1971 was an exceptionally favorable year for egg-laying, I assume that during an average year less than 10% of the potential egg production survives to become first-instar larvae in October. These populations are, therefore, potentially capable of rapid population changes, depending on summer weather conditions. The percent population increases from the 1968 to 1971 year-classes should, therefore, be largely independent of absolute population size, which they are not (Fig. 17); rather, the least abundant genera increased the most. This may be because the least abundant genera (*Pseudodiamesa*, *Heterotrissocladius*, and *Lauterbornia*) are also those that emerge earliest, and would be favored by an early and mild summer.

In conclusion, the fact that numbers dying between April and July were proportional to numbers present, and that population increases from 1968 to 1971 were inversely correlated with population size, suggest that density-dependent factors control population size. But the overriding importance of summer weather to emergence and egg-laying, the likelihood that char take a relatively constant quantity of prey in July–August, the low proportion of primary production assimilated by chironomids, and the very low mortality throughout larval life, all indicate that density-independent factors may limit chironomid populations in Char Lake to a level low enough that density-dependent effects are relatively unimportant.

Population Stability

One factor that tends to stabilize chironomid energy flow is the detritus food source. Unlike the seasonal cycles in chironomid growth due to varying phytoplankton production and sedimentation in Lake Esrom (Jónasson 1972), there are no such growth cycles in Char Lake. Of the some 450 kcal m^{-2} in the metabolically active pool, 115 kcal m^{-2} yr^{-1} are respired (Welch and Kalff 1974). Chironomid energy flow is 5–10 kcal m^{-2} yr^{-1} (Table 10). Total benthic macroinvertebrate energy flow is about 20 kcal m^{-2} yr^{-1} (Rigler 1974), nearly all through detritus feeders. Despite the strongly seasonal nature of primary production, therefore, the relatively large detritus pool provides a stable food base for detritivores.

Another stabilizing factor may be the presence of both 2- and 3-yr life cycles. If all chironomid species had identical generation times, a particularly unfavorable summer for emergence such as occurred in 1972 would result in greatly reduced chironomid production the spring and summer that that particular year-class was to emerge. But with both 2- and 3-yr species present, an unfavorable summer does not result in a great oscillation of production.

Implications for Future Work

The steady increase in chironomid populations for the year-classes 1967–1971 shows that to define "average" parameters for Char Lake chironomids, or even to delimit the magnitude of oscillation, would require annual population data spanning at least a decade. This implies that the usual 1–2-yr impact studies designed to define background conditions prior to man-induced alteration in the arctic are inadequate for better than order-of-magnitude estimates of chironomids, a key group in all lakes. Several long-term studies of representative arctic lakes may be of more value than a larger number of short studies. For chironomids, Fig. 18 suggests that these populations would be best sampled near the end of larval life, when the larvae are large but have not undergone the spring and summer char predation. However, midwinter sampling requires a considerable logistical base, and an annual early July sample would also give a good estimate of chironomid populations. In July, temperatures are above freezing, the ice provides a good working surface for coring, diving is relatively easy, light is good, and all three zones can be sampled simultaneously. By screening and sugar-floating the samples, or "crushing" them, and picking only large larvae by eye, yearly fluctuations in cohort strength could be monitored with much less effort than required by year-round sampling

of all stages. Measurements of emergence could be added to give a reasonably complete picture of chironomid production ecology.

Acknowledgments

Many people have contributed to this work. Support staff within the Department of Zoology, University of Toronto were especially helpful. A. Atagotaluk, M. Charlton, E. Ashcroft, S. Scholz, L. Wong, P. Hesse, F. Khan, and J. Lynch provided field and laboratory assistance. C. Charlton sorted most of the larvae. D. R. Oliver provided valuable advice, discussion, and the taxonomic expertise necessary to carry out the investigation. B. Shuter and A. Sreedharan performed the statistical analyses. F. H. Rigler was particularly generous with support and discussion throughout the study. I thank D. R. Oliver, R. O. Brinkhurst, P. Symons, O. Sæther, K. Patalas, and D. Rosenberg for reviewing the manuscript. The data and specimens are available should anyone wish to continue or extend this work.

BERG, K., P. M. JONASSON, AND K. W. OCKELMANN. 1962. The respiration of some animals from the profundal zone of a lake. Hydrobiologia 19: 1–40.

DAVIES, I. 1974. Selective feeding in some Arctic Chironomidae. Ver. Int. Verein. Limnol. 19.

EDWARDS, R. W. 1958. The relation of oxygen consumption to body size and to temperature in the larvae of *Chironomus rapirius* Meigan. J. Exp. Biol. 35: 383–395.

HAMILTON, A. L., W. BURTON, AND J. F. FLANNAGAN. 1970. A multiple corer for sampling profundal benthos. J. Fish. Res. Board Can. 27: 1867–1869.

HOLETON, G. F. 1973. Respiration of Arctic char (*Salvelinus alpinus*) from a high arctic lake. J. Fish. Res. Board Can. 30: 717–723.

JOHNSON, M. G. 1974. Production and productivity, p. 46–64. *In* R. O. Brinkhurst [ed.] The benthos of lakes. The MacMillan Press Ltd., London. 190 p.

JÓNASSON, P. M. 1972. Ecology and production of the profundal benthos in relation to phytoplankton in Lake Esrom. Oikos Suppl. 14: 1–148.

KONSTANTINOV, A. S. 1958. Connection between gas exchange and temperature, p. 91–108. *In* Biology of chironomids and their cultivation. Proc. Saratov Branch All-Union Res. Inst. Lake and River Fish. 5. (Transl. from Russian by Fish. Res. Board Can. Transl. Ser. No. 2044, 1972).

LASENBY, D. C., AND R. R. LANGFORD. 1972. Growth, life history and respiration of *Mysis relicta* in an Arctic and temperate lake. J. Fish. Res. Board Can. 29: 1701–1708.

MCCAULEY, V. J. E., AND K. TSUMURA. 1974. Calorific values of Chironomidae (Diptera). Can. J. Zool. 52: 581–586.

OLIVER, D. R. 1968. Adaptations of Arctic Chironomidae. Ann. Zool. Fenn. 5: 111–118.

PLATZER-SCHULZ, I. 1970. On respiration of various lifestages of *Chironomus strenzkei* Fittkau (Diptera). Z. Vergl. Physiol. 67: 179–185.

RIGLER, F. H. 1972. The Char Lake Project, a study of energy flow in a high Arctic lake, p. 287–300. *In* Z. Kajak and A. Hillbricht-Ilkowska [ed.] Productivity problems of freshwaters. Warszawa-Krakow, Polish Scientific Publishers, Warsaw.

RIGLER, F. H., M. E. MACCALLUM, AND J. C. ROFF. 1974. Production of zooplankton in Char Lake. J. Fish. Res. Board Can. 31: 637–646.

ROFF, J. 1972. *Limnocalanus* production. Char Lake Proj. Annu. Rep. p. 27–31.

SÆTHER, O. 1975. Neartic and Palaerctic *Heterotrissocladius* (Diptera: Chironomidae). Bull. Fish. Res. Board Can. 193: 67 p.

SCHINDLER, D. W., H. E. WELCH, J. KALFF, G. J. BRUNSKILL, AND N. KRITSCH. 1974. Physical and chemical limnology of Char Lake, Cornwallis Island (75°N lat.). J. Fish. Res. Board Can. 31: 585–607.

SCHOLANDER, P. F., W. FLAGG, V. WALTERS, AND L. IRVING. 1953. Climatic adaptation in Arctic and tropical poikilotherms. Physiol. Zool. 26: 67–92.

TAUBE-NAUWERCK, I. 1972. Cyclopoids. Char Lake Proj. Annu. Rep. p. 48–52.

WATERS, T. F. 1969. The turnover ratio in production ecology of freshwater invertebrates. Am. Nat. 103: 173–185.

WELCH, H. E. 1967. Energy flow through the major macroscopic components of an aquatic ecosystem. Ph.D. Thesis. University of Georgia, Athens, Ga. vi + 97 p.

1968. Relationships between assimilation efficiencies and growth efficiencies for aquatic consumers. Ecology 49: 755–759.

1973. Emergence of Chironomidae (Diptera) from Char Lake, Resolute, Northwest Territories. Can. J. Zool. 51: 1113–1123.

WELCH, H. E., AND J. KALFF. 1974. Benthic photosynthesis and respiration in Char Lake. J. Fish. Res. Board Can. 31: 609–620.

WINBERG, G. G. 1971. Symbols, units and conversion factors in the studies of freshwater productivity. Int. Biol. Programme (IBP) Spec. Publ. 23 p.

A Bioenergetics-Based Model for Pollutant Accumulation by Fish. Simulation of PCB and Methylmercury Residue Levels in Ottawa River Yellow Perch (*Perca flavescens*)[1]

R. J. NORSTROM,[2] A. E. MCKINNON, AND A. S. W. DEFREITAS

National Research Council of Canada, Division of Biological Sciences, Ottawa, Ont. K1A 0R6

NORSTROM, R. J., A. E. MCKINNON, AND A. S. W. DEFREITAS. 1976. A bioenergetics-based model for pollutant accumulation by fish. Simulation of PCB and methylmercury residue levels in Ottawa River yellow perch (*Perca flavescens*). J. Fish. Res. Board Can. 33: 248–267.

A pollutant accumulation model is developed which successfully predicts concentrations of PCBs and methylmercury in tissues of yellow perch (*Perca flavescens*) from the Ottawa River, Canada. The model is based on pollutant biokinetics coupled to fish energetics. The expression for metabolic rate includes a growth dependent term for estimating the contribution to metabolism of seasonal and annual growth in each age-class. Uptake of pollutant from food is based on caloric requirements for respiration and growth coupled to concentration of pollutant in food and its assimilation efficiency from the diet. Uptake of pollutant from water is based on flow of water past the gills for respiration coupled with concentration of pollutant in water and the efficiency of its assimilation by gills. Pollutant clearance is related to body weight raised to the power of −. 58, but is independent of metabolic rate. Under steady state conditions of chronic exposure, the predicted ratio of uptake to clearance is roughly constant at all weights, and the slope of a curve of log pollutant concentration in tissues vs. log body weight can be used to establish the exponent of body weight for clearance.

NORSTROM, R. J., A. E. MCKINNON, AND A. S. W. DEFREITAS. 1976. A bioenergetics-based model for pollutant accumulation by fish. Simulation of PCB and methylmercury residue levels in Ottawa River yellow perch (*Perca flavescens*). J. Fish. Res. Board Can. 33: 248–267.

Les auteurs développent un modèle d'accumulation de polluants pouvant prédire avec succès les concentrations de PCB et de mercure-méthyl dans les tissus de la perchaude (*Perca flavescens*) de la rivière Outaouais au Canada. Le modèle est fondé sur la biocinétique couplée à l'énergétique des poissons. L'expression pour le taux métabolique inclut un terme dépendant de la croissance et servant à estimer ce que la croissance saisonnière et annuelle dans chaque classe d'âge contribue au métabolisme. L'assimilation du polluant provenant de la nourriture est fondée sur les calories requises pour la respiration et la croissance, et sur la concentration du polluant dans la nourriture et l'efficacité avec laquelle ce dernier est extrait du régime alimentaire. L'assimilation du polluant à partir de l'eau dépend du débit d'eau irrigant les branchies pour la respiration couplé à la concentration du polluant dans l'eau et l'efficacité avec laquelle il est assimilé par les branchies. La clairance du polluant est fonction du poids corporel élevé à la puissance de −.58, mais est indépendante du taux métabolique. Dans les conditions d'équilibre d'une exposition chronique, le rapport prévu de l'assimilation à la clairance est à peu près constant à tous les poids, et on peut utiliser la pente d'une courbe logarithmique de la teneur du polluant dans les tissus vs le logarithme du poids corporel pour déterminer l'exposant du poids corporel applicable à la clairance.

Received August 12, 1975
Accepted November 14, 1975

Reçu le 12 août 1975
Accepté le 14 novembre 1975

IN addressing the problem of pollutant bioaccumulation in aquatic habitats, it seems reasonable to propose that an organism will obtain its pollutant from eating contaminated food and also from breathing contaminated water. There is much evidence in the literature that the bioassimilation efficiency from water and food is directly related to the lipophylicity of the pollutant, strongly lipophylic compounds like DDT or PCBs being assimilated at maximum efficiency compared to amphyphilic compounds like methylmercury (Reinert et al. 1974). Both food and

[1]Carried out as part of the Ottawa River Project, a joint study by the National Research Council and the University of Ottawa. Issued as NRCC No. 14972.

Printed in Canada (J3947)
Imprimé au Canada (J3947)

[2]Present address: Canadian Wildlife Service, Toxic Chemicals Division, Ottawa, Ont. K1A 0H6.

water uptake vectors should be quantitatively related to metabolic rate which, in turn, can be quantitatively related to body size (deFreitas and Hart 1975; Murphy and Murphy 1971), growth rate, and environmental temperature (Reinert et al. 1974). The uptake rate of pollutants by aquatic biota should, therefore, fall within limits set by species-specific factors controlling metabolic rate and growth, as modified by environmental factors such as water temperature and food availability.

Once the pollutant enters the circulation of an organism and becomes bound to various tissue components, its clearance from the whole organism should be directly related to the turnover of the tissue components which in turn should be relatable to metabolic rate or some other species-specific, time dependent, and definable function such as body size and/or adiposity. An energy utilization model based on the general principles outlined above, has been applied to the accumulation of methylmercury in northern pike (*Esox lucius*) (Fagerström and Åsell 1973; Fagerström et al. 1974). The predicted and actual methylmercury concentrations agreed well except at low fish weights of 300 g or less. Sensitivity analysis of a more detailed model based on metabolic parameters led Fagerström and Åsell (1973) to conclude that only the part of the model relating to uptake of methylmercury from water was low in realism. A similar type of model was used by Norstrom et al. (1975) to produce "best fits" to data for residue levels of polychlorinated biphenyls (PCBs), DDT, and methylmercury in four species of fish in the Ottawa River. Adjusting the efficiency of uptake from food was usually necessary to achieve a fit to the measured values of pollutant concentration in fish. In most cases the predicted clearance half-lives were insensibly long, indicating the need for further modifications of the overall equation, particularly the clearance function.

The present report describes a pollutant accumulation model developed on the basis of fish energetics coupled to recent information on pollutant biokinetics. The reality of the model's formulation and parameter values is tested by comparing its simulation of PCB and methylmercury accumulation to the actual values observed in a natural population of yellow perch (*Perca flavescens*) in the Ottawa River. The Glossary should be referred to for formal definitions of symbols used in the text.

Bioenergetics

Since pollutant uptake should be related to the flow of energy into the fish, both in the form of food and in the form of oxygen from water, the model must first of all be able to adequately represent the bioenergetics and growth of fish. Fortunately, several authors have critically reviewed the enormous body of data in this field (Parker and Larkin 1959; Paloheimo and Dickie 1965, 1966a, b; Beamish and Dickie 1967; Warren and Davis 1967; Kerr 1971a; Beamish et al. 1975).

In the following section, bioenergetic concepts, reviewed by the above authors, are discussed in terms of assembling an energetics based model suitable for pollutant bioaccumulation by fish populations in the real world.

The balanced energy equation

$$e_f R = Q + dW/dt \qquad (1)$$

states that the energy of the ingested ration, corrected for fecal and nonfecal losses to give metabolizable ration $e_f R$, is equal to the sum of total metabolic rate Q, and growth rate dW/dt, all terms being expressed in energy units per unit time. In carnivorous fish there appears to be relative constancy in the fraction of the ration lost as feces and as nitrogenous compounds secreted in urine and across the gill membrane, resulting in a net energy intake efficiency (e_f) from food of ca. 0.8 (Beamish et al. 1975).

It is also generally accepted that the empirical expression

$$Q = \alpha W^{\gamma} \qquad (2)$$

where α is the "level" of metabolism (the respiration rate of a 1-g fish) and the body weight exponent γ is ca. 0.8 for most fish gives a reasonable approximation to the body weight dependence of total energy metabolism at any level between standard metabolism Q_s, and active, Q_{max} (Paloheimo and Dickie 1965). Winberg (1956) implies that equation (2) represents all energy expenditures, most of his data being taken from short-term respiration studies. As a result, equation (2) may be most applicable to growth-unrelated (routine) metabolism.

The value of α varies with temperature, but at energy expenditure levels above standard the dependence may change, and at active levels may be very species dependent (Fry 1957). Winberg considers the Krogh (1941) "normal curve" to be adequate for comparison of metabolic rates at different temperatures; however, Beamish (1964) has pointed out that many studies of standard oxygen consumption, Q_s, have not taken into account the metabolism associated with spontaneous activity, Q_a, which is itself highly temperature dependent for most species. Nevertheless, Winberg's values of α, which correspond to

"routine" metabolism, Q_r, where $Q \approx 1.7\ Q_s$, are often successful at predicting respiration rates over at least part of the normal temperature range of various fish (Solomon and Brafield 1972).

Active metabolism, Q_{max}, cannot be predicted a priori from Q_r or Q_s. The difference $Q_{max} - Q_s$ has been defined by Fry (1957) as *scope for activity*. Warren and Davis (1967) defined the related concept, *scope for growth*, which is a restatement of the balanced energy equation in terms of food conversion efficiency: $dW/dt \leqslant e_f R - Q$. Since there is expenditure of energy associated with growth, these two concepts can be combined; that is, $Q_{max} - Q_s$ can be considered the scope for activity-related plus growth-related energy expenditures, or the scope for excess energy utilization.

The body weight exponent, γ, in equation (2) has been found to be the same or similar at various levels of metabolism, including active, for *Salvelinus fontinalis* (Job 1955) and *Onchorhynchus nerka* (Brett 1965). If this result can be generalized, we are justified in considering any level of routine metabolism, Q_r, to be equal to $\alpha_r W^\gamma$, where $\alpha_s < \alpha_r < \alpha_{max}$.

In the analytical model on growth efficiency of *S. fontinalis*, Kerr (1971a) describes total metabolism, Q, as the sum of standard metabolism, Q_s, energy cost specific to utilization of food, Q_c, energy cost of spontaneous activity, Q_a, and the energy cost of foraging, Q_f.

$$Q = Q_s + Q_a + Q_c + Q_f \tag{3}$$

where Q, Q_s, and Q_a are given by equations of the form (2). In the present discussion, "low routine" metabolism, or Q_{lr}, is defined by

$$Q_{lr} = Q_s + Q_a = \alpha_{lr} W^\gamma \tag{4}$$

where Q_a is considered to represent all activity-related metabolism, including Q_f. Therefore, the balanced energy equation can be written as

$$e_f R = Q_{lr} + Q_c + dW/dt \tag{5}$$

Beamish et al. (1975) have proposed a scheme where metabolizable or useful energy is the fraction of the total food energy remaining after fecal losses, specific dynamic action (SDA), and nonfecal losses have been subtracted. In practice, the SDA associated with a maintenance ration (low routine metabolism) is included in estimates of α_{lr}, since metabolized energy and SDA are indistinguishable in terms of respired oxygen requirements. However, the SDA associated with utilization of food for growth adds an additional oxygen requirement which is proportional to that fraction of the metabolizable energy used for growth, and, therefore, growth rate. If we assume that this additional oxygen requirement constitutes the major portion of Q_c, and introduce the proportionality constant, β, we have

$$Q_c = \beta(dW/dt) \tag{6}$$

Noting that net maintenance ration, $e_f R_{maint}$, can be equated to low routine metabolism, Q_{lr} (Brown 1957; Paloheimo and Dickie 1966a), we can interpret equations (5) and (6) in terms of the various definitions of conversion efficiencies of food to body substance. Thus, gross conversion efficiency is defined as

$$E_g = \frac{dW/dt}{R} = \frac{(dW/dt)e_f}{Q_{lr} + Q_c + dW/dt} \tag{7}$$

If net conversion efficiency is defined as

$$E_n = \frac{dW/dt}{R - R_{maint}} = \frac{(dW/dt)e_f}{Q_c + dW/dt} \tag{8}$$

then from equation (6), β is related to E_n by

$$\beta = \frac{e_f}{E_n} - 1 \tag{9}$$

The only factor in Kerr's partitioning of metabolism which cannot be modeled directly in our system is Q_f, the energy used in foraging. We must fall back on some form of equation (2), to account for all growth-unrelated energy expenditures (low routine metabolism, equation (4)). Estimates of low routine metabolism from which α_{lr} values are derived certainly include a considerable portion of the "normal" swimming activity of a fish which would result in prey capture (Kerr 1971b), and during the active growth season prey is more abundant, helping to balance out the increased energy cost of foraging for extra food necessary for growth. In our formulation of the overall energy equation, the energy cost of foraging will be absorbed by the values assigned to the α and β parameters.

To assemble the bioenergetics model, the following points have been taken from the preceding discussion:

1. Total metabolism is the sum of "low routine" metabolism, Q_{lr} (corresponding to a maintenance ration), and growth related metabolism, Q_c.

2. Equation (2) adequately describes the dependence of Q_{lr} on body weight at a given set of environmental conditions.

3. Q_c is directly proportional to growth rate, as in equation (6).

4. Both food and deposited tissue are assumed

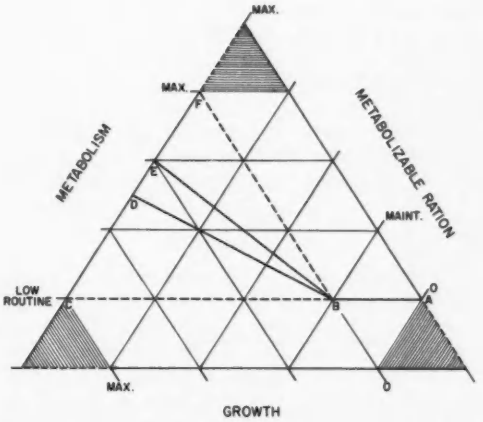

FIG. 1. Metabolism, growth rate, and metabolizable ration predicted by equations (10) and (11) for a hypothetical fish where maximum (active) metabolism is 3 times low routine metabolism. Metabolizable ration is total ration corrected for fecal and nonfecal (nitrogenous waste) losses.

to have a caloric equivalent of 1 kcal/g wet weight.

These points do not arise from a precise understanding of metabolic processes, but they appear to be an adequate description of fish bioenergetics in terms of providing a basis for writing the required mathematical equations. The bioenergetics model can, therefore, be written as:

$$Q = \alpha_{lr} W^{\gamma} + \beta(dW/dt) \tag{10}$$

and

$$R = \frac{1}{e_f}[\alpha_{lr} W^{\gamma} + (\beta + 1)(dW/dt)] \tag{11}$$

where $(\beta + 1)\,(dW/dt)$ is the sum of the caloric content of the deposited tissue and the energy required to deposit the tissue.

Figure 1 illustrates the relations between metabolism, growth rate, and ration predicted by equations (10) and (11) for a hypothetical fish where $Q_{max} = 3Q_{lr}$. The scale for all three axes is equivalent to multiples of Q_{lr} since $e_f R_{maint}$ and catabolism at zero ration are all considered equal to low routine metabolism (Q_{lr}). Metabolizable ration is $e_f R$. The dashed lines on the axes and the hatched triangular areas next to them define conditions that cannot apply: negative ration, metabolism greater than Q_{max}, and growth rate greater than $(dW/dt)_{max}$.

To satisfy the balanced energy equation (1), metabolism, ration, and growth must be defined by the line A, B, or the surface B, C, F. The line A, B represents the situation where, as ration increases from zero to maintenance, less body substance is required to maintain "low routine" metabolism. Above a maintenance ration, the excess ration may be apportioned to metabolism and growth. The line B, F is the extreme situation where all excess metabolizable energy of the ration is metabolized, and B, C is an equally extreme case where all excess ration is converted to body substance. In fact, fish are most likely to exist somewhere on the surface of B, D, E where B, D represents a net conversion efficiency (E_n) of 41% ($\beta = 1.0$), and B, E a net conversion efficiency of 27% ($\beta = 2.0$) independent of ration (Warren and Davis 1967) assuming an assimilation efficiency of ingested calories (e_f) of 0.82. If net conversion efficiency is dependent on ration, a curved rather than a straight line would be observed, but still on the surface B, D, E. Evidence will be presented later, showing that conditions defined by B, D (Fig. 1) represent the most likely and generally valid situation.

Pollutant Bioaccumulation

For a pollutant bioaccumulation model to have general and easy applicability to real ecosystems it must be able to use information that can be readily derived from relatively unsophisticated field data. To extend the bioenergetics model to bioaccumulation of pollutant, it is assumed that uptake from water is proportional to total respiration (Q) and uptake from food is proportional to ingested ration (R). The latter relation is easily defined as

$$(dP/dt)_f = e_{pf} C_{pf} R \tag{12}$$

where e_{pf} is efficiency of pollutant uptake from food, C_{pf} is the concentration of pollutant in the food, and $(dP/dt)_f$ is the rate of pollutant uptake from food by fish (weight/unit time).

The rate of pollutant uptake from water, $(dP/dt)_w$, is, in a similar fashion, related to the flux of water past the gill surface. This is a function not only of Q, but also of the concentration of oxygen in the water, C_{ox}, and the efficiency of oxygen transfer across the gills, e_{ox}. Thus, for pollutant uptake from water

$$\begin{aligned}(dP/dt)_w &= e_{pw} C_{pw} V \\ &= e_{pw} C_{pw} (Q/e_{ox} \cdot C_{ox} \cdot q_{ox})\end{aligned} \tag{13}$$

where V is the volume of water flowing past the gills per unit time, e_{pw} is the efficiency of pollutant transfer across the gills, C_{pw} is the concentration of pollutant in water, and q_{ox} is the caloric equivalent of inspired oxygen.

The form of the clearance equation presents considerably more difficulty. Whole body clearance of methylmercury (Järvenpää et al. 1970; Matida et al. 1971; Burrows and Krenkel 1973) and organochlorine compounds (Robinson 1967) has been shown to follow first order kinetics under various sets of physiological and environmental conditions. Initial studies in our laboratory (deFreitas et al. 1974), however, indicated that fractional clearance rate of methylmercury decreased with body weight, and it was proposed that metabolic rate might be the dominant factor in controlling whole body clearance. This, in accordance with equation (10), led to a model formulation where clearance was proportional to $W^{\gamma-1} + \beta(dW/dt)\ W^{-1}$ which was unsuccessful in predicting reasonable clearance values when applied to real world data (Norstrom et al. 1975). Further experiments on the effect of body size, water temperature, and growth rate were performed in our laboratory. The results are reported in detail elsewhere (deFreitas et al. 1975; Sharpe et al. 1975). No effect of temperature on clearance of methylmercury was observed when groups of goldfish (body size, 10 g wet weight) were maintained at 5 C, 10 C, and 20 C. No effect of metabolic rate on fractional clearance was observed when groups of fish at 20 C were fed rations ranging from maintenance to ad libitum levels (corresponding to a three- to fourfold range in metabolic rate computed from growth). The results from these experiments demonstrate that the dominating factor controlling methylmercury clearance is not metabolic rate but rather allometric disproportions in clearance-related rate processes.

It was, therefore, obvious that, although body weight affected clearance, the effect could not be attributed to metabolic rate changes. Fractional clearance data from several experiments on goldfish at different temperatures and diets are shown plotted vs. body weight in Fig. 2. One value for northern pike (*E. lucius*) from Järvenpää et al. (1970) is included. There are the expected individual variations, but it is clear that fractional clearance of methylmercury is proportional to $W^{-0.58}$, independent of metabolic rate, ration, and temperature. On this basis, the rate of clearance can be written as

$$(dP/dt)_{cl} = -k_{cl}PW^{\zeta} \qquad (14)$$

where k_{cl} is the clearance coefficient, dependent only on the type of pollutant and perhaps species, P is the body burden of pollutant, and ζ is an exponent with a value probably between -0.2 and -0.8.

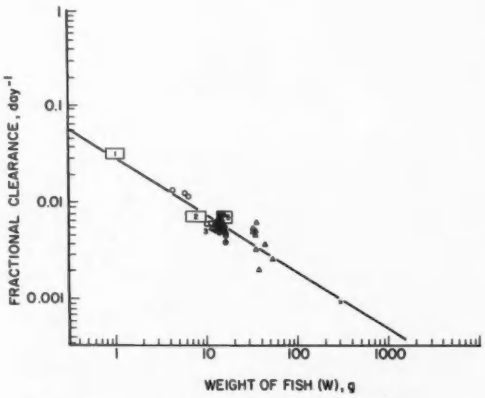

FIG. 2. Whole body clearance of methylmercury chloride from goldfish (*Carassius auratus*) at various weights and temperatures (Sharpe et al. 1975). The fish were kept on a maintenance diet. Box no. 1, 5 fish at 19–24 C; no. 2, 6 fish at 19–24 C; no. 3, 18 fish at 5 C; no. 4, 19 fish at 20 C; no. 5, 4 fish at 19–24 C. The size of the box indicates standard error estimates for each group of fish. ○, ●, △ represent data for single fish at 20 C, X represents data for northern pike (*Esox lucius*) at 7.1 C, reported by Järvenpää et al. (1970).

The applicability of equation (14) to the clearance of organochlorine compounds is somewhat conjectural. There is no experimental evidence in the literature to either contradict or confirm this type of body weight dependence. Nevertheless, it will be shown that the dependence of PCB body burden or concentration on body weight is consistent with the form of equation (14).

The complete model equation is the sum of equations (12), (13), and (14) with substitutions for Q and R from equations (10) and (11),

$$dP/dt = \frac{e_{pw}C_{pw}}{e_{ox}C_{ox}q_{ox}}\left(\alpha_{lr}W^{\gamma} + \beta\frac{dW}{dt}\right) + \frac{e_{pf}C_{pf}}{e_f} \times \left[\alpha_{lr}W^{\gamma} + (\beta + 1)\frac{dW}{dt}\right] - k_{cl}pW^{\zeta} \qquad (15)$$

Parameter Value Determination

1. *Food conversion efficiency for growth (β) and growth rate (dW/dt)*

Three studies can be quoted that give values for β. From Fig. 8 in the study of Solomon and Brafield (1972) on the complete energy budget of the European perch (*Perca fluviatilis*), it can be deduced that

$$Q - Q_{lr} = Q_e \approx 0.4(R - R_{maint}) \qquad (16)$$

where $Q_{ir} = e_f R_{maint}$. Using equations (1) and (6) we obtained the form of equation (16) with $0.4 \approx \beta e_f/(1 + \beta)$. Taking Solomon and Brafield's value of 0.83 for e_f, we have $\beta = 0.93$.

Niimi and Beamish (1974) studied the bioenergetics and growth of largemouth bass (*Micropterus salmoides*). They found growth in kilocalories as a function of ration to be expressed by

$$dW/dt = a + bR \qquad (17)$$

where b varied from 0.4 to 0.6, average 0.48, independent of body weight and temperature. The values of a were roughly proportional to $W^{0.8}$ at each temperature. By reference to equations (1) and (6), we again can make a direct comparison of the experimental data with our model. We find that $b = e_f/(1 + \beta)$ and $a = -e_f R_{maint}/(1 + \beta)$. Taking the values $e_f = 0.82$ and $b = 0.395$ for 50-g fish at 25 C where the data are most complete, we can calculate $\beta = 1.08$. Using this value of β and $a = -0.207$ kcal/day for the same set of data, R_{maint} is calculated to be 0.398 kcal/day, agreeing well with the maintenance energy requirement of 0.35 kcal/day given in Niimi's table 3.

Johnson (1966) studied the food conversion efficiency of northern pike (*E. lucius*) under natural temperature conditions over a year. After subtracting the maintenance requirements, he calculated an annual mean value for the "overall efficiency of utilization," or E_n in our terminology, to be 0.437 on a weight of food to weight of fish basis. Taking $e_f = 0.82$, we calculate $\beta = 0.88$ from equation (9). The data of Warren and Davis (1967) demonstrate that net efficiencies can vary with season and size of ration, which from equation (9) implies that β will vary as well. However, since in the natural environment one would expect net efficiencies to be highest during the growing season, it appears safe to assume an optimum value of 1.0 for β, as found in the first two studies quoted above.

To study the effect of temperature and oxygen concentration as well as discontinuous growth on pollutant uptake, growth was treated in two ways: annual and weekly increments. Field data on annual and seasonal growth were taken from Qadri and Rubec (1974) for the same population of *Perca flavescens* which was analyzed for mercury and organochlorine residues. Annual increments were modeled by the von Bertalanffy (1938) equation

$$L = a(1 - e^{-b(t-c)}) \qquad (18)$$

where L is the length in millimeters and t is the age in years. Assuming a length at infinity, a, of 343 mm, the parameters b and c were fitted by computer. To convert growth in length to a weight and subsequent energy basis, the equation

$$W_v = \lambda L^{\eta} \qquad (19)$$

was fitted by least mean squares to the log/log transformation of the length/weight data obtained from the fish used for chemical analysis. The parameters a, b, c, λ, and η are given in Table 1.

Qadri and Rubec (1974) found that *Perca flavescens* in the Ottawa River had a growing season of mid-May to mid-September. The earlier age-classes continued to grow throughout the whole season, whereas the later age-classes stopped growing sometime in August. The shape

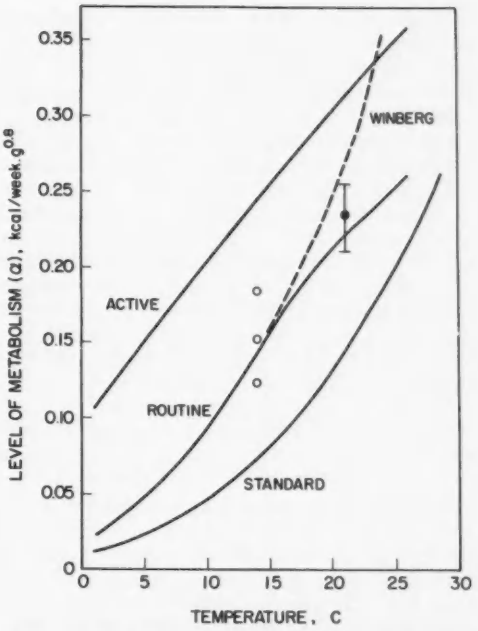

FIG. 3. Values for standard, routine, and active levels of metabolism as a function of temperature. Standard and active levels determined from data of Ferguson as given in figs. 22 and 27 of Fry (1957). The level of low routine metabolism as used in the present model (continuous line) is the same as that of Winberg (1956) up to 15 C, but falls below Winberg's values (dashed line) above 15 C. ○ represents data from Solomon and Brafield (1972) for European perch (*Perca fluviatilis*) and ⏚ represents a mean value calculated from the maintenance ration of yellow perch (*Perca flavescens*) reported by Moore (1941), the bars corresponding to a weight range of 1.6–4 g.

TABLE 1. Parameter values for the simulations of bioaccumulation of methylmercury and PCBs by yellow perch (*Perca flavescens*)[a].

Parameter[b]	Value	
	General parameters	
β	1.0	
e_f	0.82	
e_{ox}	0.75	
q_{ox}	3.42 kcal/g	
γ	0.81	
ζ	−0.58	
	Parameters dependent on species	
a	343 mm	
b	0.00313 wk^{-1}	
c	−26 wk	
λ	17.4×10^{-6} g $mm^{-\eta}$	
η	3.02	
	Parameters dependent on pollutant	
	methylmercury	PCBs[c]
e_{pw}	0.12	0.75
C_{pw}	4×10^{-12} g/g	2.5×10^{-12} g/g
e_{pf}	0.80	0.80
C_{pf}	33×10^{-9} g/g	130×10^{-9} g/g
k_{ci}	0.202 $g^{-\zeta}$ wk^{-1}	0.283 $g^{-\zeta}$ wk^{-1}

[a]The "constant normalized" parameters $||\alpha_{lr}||$ and $||C_{ox}||$ used in the simulations for each age-class are given in the first two columns of Table 5.
[b]For definition of symbols, see Glossary.
[c]As Aroclor 1254.

of the growth curve in weight was sigmoid (see also Fortin and Magnin 1972). To use this information, it was assumed that no growth or loss of weight (no net calorie change) occurred outside the growing season, and the approximate shapes of the seasonal growth curves for each age-class were fitted graphically to the annual growth increments previously determined. The result is shown in the upper curve of Fig. 5.

2. *Routine metabolic rate coefficient (α_{lr}) and the body weight exponent (γ) for routine metabolism*

The data of R. G. Ferguson on the oxygen consumption of *Perca flavescens* at standard and active levels of metabolism (assuming air saturation of the water) given in fig. 22 and fig. 27 of Fry (1957) were used to help determine the appropriate values of α as a function of temperature. If it is assumed that $\gamma = 0.81$, Ferguson's curves, which were based on 5-g fish, can be transformed into α values using equation (2), as shown in Fig. 3. We now have an "envelope" within which the routine metabolism corresponding to a maintenance ration must fit. Equation 7.3.4 and table 1 in Winberg (1956) allow an estimate of routine metabolism as a function of temperature to be made based on data for many species of freshwater fish. Solomon and Brafield (1972) have shown that Winberg's α value of 0.3 ml of oxygen per $h \cdot g^{0.81}$ (0.24 kcal/$wk \cdot g^{0.81}$) is quite accurate for predicting metabolism of *Perca fluviatilis* on a maintenance ration when corrected to the appropriate temperature of 14 C. Winberg's α values are, therefore, equivalent to our definition of level of low routine metabolism, α_{lr}. Since *Perca flavescens* is a closely related species, we show these α_{lr} values plotted in Fig. 3 (solid line to 15° and dashed line from 15° to 24°).

One failure of the Winberg values is immediately seen: at temperatures above 24 C predicted low routine metabolism begins to exceed active metabolism. The explanation for this is obvious from the work of Fry (1957) and Beamish (1964) which demonstrates that routine metabolism is not a monotonic function of temperature, since spontaneous activity for many species of fish has a maximum near the preferred temperature. This phenomenon was one of the hypotheses proposed by Burkett (1974) to explain the lack of difference in methylmercury uptake by bluntnose minnows (*Pimephales notatus*) from water at 21 and 24 C. The preferred temperature of *Perca flavescens* is around 20 C (Scott and Crossman 1973), suggesting that the

curve for α_{lr} vs. temperature should begin to drop off in this region. One experimental value at 21 C, calculated from the maintenance food requirements assuming 1 kcal/g of fish, was obtained from Moore (1941). This value indicates that low routine metabolism does in fact lie below Winberg's estimates at temperatures above 20 C. With this general information, the curve for α_{lr} vs. temperature was drawn (solid line) to fall below that of Winberg beginning at 15 C, the subsequent values being estimated by assuming that low routine minus standard metabolism formed a symmetrical peak around 20 C (see fig. 6, Beamish 1964). Since temperatures much above 20 C are relatively uncommon in the Ottawa River, this estimate will not introduce significant error in calculating low routine metabolism.

3. Efficiency factors for pollutant uptake from water (e_{pw}), oxygen uptake from water (e_{ox}), pollutant uptake from food (e_{pf}) and calorie uptake from food (e_f)

We have defined e_f to take into account not only unassimilated calories, but also calories subsequently lost as nitrogenous waste during digestion and assimilation, and have accepted the value of 0.82 as given by Beamish et al. (1975). The absorption efficiency of methylmercury from the diet is assigned a value of 0.8 (table 1) based on an assessment of reported values ranging from 0.67 to 0.94 (Hannerz 1968; Suzuki and Hatanaka 1975; deFreitas et al. 1974, 1975). A value of 0.8 is also assigned to the absorption efficiency of PCBs (Södergren 1973). Values for the efficiency of pollutant uptake from water, e_{pw}, are much more difficult to estimate, since it is necessary to have some means of determining the quantity of pollutant which flows past the gill surface.

From equation (13) we can see that if the pollutant concentration in water (C_{pw}), the oxygen concentration in water (C_{ox}), and total metabolism (Q) can be measured or estimated, it is possible to determine the ratio of e_{pw} to e_{ox}. The ratio of $(dP/dt)_w$ to C_{pw} gives the volume of water "cleared" of pollutant per unit time. Similarly, the metabolic rate transformed to units of oxygen may be calculated, using equation (2) where necessary, and divided by C_{ox} (air saturated), giving the volume of water "cleared" of oxygen per unit time. The ratio of the two clearance rates is the ratio e_{pw}/e_{ox}. Several uptake studies on organochlorine compounds (largely DDT) and methylmercury studies from our own laboratory were reanalyzed in order to determine this ratio, as shown in Table 2.

Although a fairly wide range of values for the ratio e_{pw}/e_{ox} for organochlorines was found, the more definitive studies, particularly that of Murphy and Murphy (1971), indicate that these compounds may be more efficiently cleared from water than is oxygen. The estimated efficiency of oxygen clearance from water is 0.75 (Lloyd 1961), so a value of 1.33 for the ratio e_{pw}/e_{ox} corresponds to $e_{pw} = 1.0$. On this basis, five of the calculations give high values for the ratio, which is not surprising considering the probable inaccuracy of estimating all of the parameters needed to perform the calculation. It must also be remembered that in natural river water, e_{pw} may be affected by constituents of the water which are not found in aquarium experiments. Since C_{pw} for organochlorines cannot be measured in our system any more closely than the likely variation of e_{pw}, we have chosen to take $e_{pw} = e_{ox} = 0.75$.

The situation for methylmercury is undoubtedly as complex as for organochlorines. A wide range of aquarium experiments on uptake of methylmercury from various types of water including river water (deFreitas et al. 1974; deFreitas and Hart 1975) have given $e_{pw}/e_{ox} \approx 0.16$, and therefore $e_{pw} \approx 0.12$. This is in line with the work of Reinert et al. (1974) who found that methylmercury was accumulated less fast than DDT at three different temperatures. Several initial experiments with river water, the results of which are given at the bottom of Table 2, indicated that e_{pw} may be raised in natural water. This effect was both seasonal and nonreproducible, so we chose to take $e_{pw} = 0.12$ although this may well be the minimum value.

4. Caloric equivalent of oxygen (q_{ox}), concentration of dissolved oxygen (C_{ox}) and pollutant (C_{pw}) in water, pollutant concentration in fish food (C_{pf}) and fish tissue (P/W)

The Ottawa River passes through a series of rapids immediately upstream from the 3-mile reach from which the yellow perch population was sampled, and as a result is well aerated during summer as well as during the winter months. Oxygen concentration, C_{ox}, at all times of year was found to be close to air saturation values given by the equation

$$C_{ox} = 14.45 - 0.413T + 0.00556T^2 \text{ (g/g} \times 10^6\text{, 0–25 C)} \quad (20)$$

where T is the water temperature in degrees centigrade. The caloric equivalent of oxygen, q_{ox}, was taken to be 3.42 kcal/g (Winberg 1956).

The concentration of pollutants in unfiltered water was determined approximately every month

TABLE 2. Review of the experimental evidence on the efficiency of uptake of pesticides and methylmercury from water by the gills.[a]

Fish species	Wt (*g*)	Temp (*C*)	$(dP/dt)_w/C_{pw}$ (*ml water/h*)	$Q/q_{ox}C_{ox}$ (*ml water/h*)	e_{pw}/e_{ox}	Compound	Conc in water ($g/g \times 10^9$)	Source
Salvelinus fontinalis	76	14	164	832	0.317	DDT	0.003	Macek and Korn 1970
Carassius auratus	1.8	22	182	110	1.66	Clophen A 50	10 to 500	Hattula and Karlog 1973
Salmo salar	5.2	15	7.96	109	0.073	DDT	1000	Premdas and Anderson 1963
Lepomis macrochirus	5.75	20	372	206	1.81	DDT	30	Gakstatter and Weiss 1967
Carassius auratus	5.4	20	373	197	1.90	DDT	30	
Notemigonus crysoleucas	1.86	23	106	114	0.92	DDT	0.2	Reed 1969
Gambusia affinis	0.088	23?	3.55	9.86	0.36	DDT	0.041	Murphy 1970
	0.151	23?	4.83	15.10	0.32	DDD	0.055	
	0.089	23?	3.65	10.14	0.36	DDE	0.032	
Gambusia affinis	0.1 to 1.0	20	$20.9W^{0.75}$	$15.3W^{0.68}$	1.36	DDT	0.041	Murphy and Murphy 1971
		5	$7.6W^{0.77}$	$4.7W^{0.71}$	1.61	DDT	0.041	
Catostomus commersoni,	2	15	8.8	54.2	0.16	[b]CH_3Hg^+	0.01 to 1.0	deFreitas and Hart 1975; de Freitas et al. 1974
	10	15	29.8	196.3	0.15			
Monostoma macrolipidotum,	100	15	172.0	1239	0.14			
	3.4	23	42.5	186	0.23			
Notemigonus crysoleucas,	3.4	10	5.5	39.6	0.14			
Esox lucius,	2	15	26.4	54.2	0.49	[c]CH_3Hg^+		
Ictalurus nebulosus	10	15	90	196.3	0.46			

[a]For definition of symbols used, see Glossary. Columns headed $(dP/dt)_w/C_{pw}$ and $Q/q_{ox}C_{ox}$ give milliliters of water "cleared" of pollutant and oxygen per hour, respectively, and the ratio of these two columns gives the ratio of pollutant uptake efficiency to oxygen uptake efficiency, e_{pw}/e_{ox}. Q was calculated from equation (2).

[b]These experiments were performed in deionized tap water, ionically resynthesized to resemble river water.

[c]These experiments were performed using river water.

from May 1972 to September 1973 (Norstrom and Brownstein 1974). Initially, several sites were sampled, but little variation in concentration with geographical site was found. In 1973, no difference in concentration could be found in sites well upstream of the sampling area compared to the test section, and it was concluded that a "background" level had been reached for both organochlorine and mercury. The concentration of methylmercury in water (C_{pw}) was estimated to be in the order of 4×10^{-12} g/g prior to 1973. The effect of changing this value to 2 and 8×10^{-12} g/g will be shown later. The majority of the values of C_{pw} for PCBs were found to be in the $1.2–4.0 \times 10^{-12}$ g/g range, and 2.5×10^{-12} g/g was chosen as a median value.

Studies of the food of perch in the Ottawa River (Qadri and Rubec 1974) showed that invertebrates were the main dietary components to at least age-class 4+. The average volume percent in the diet was: Crustacea, 19%; Insecta (principally chironimidae), 38%; and small gastropods, 16%. Small fish formed only 8% of the diet, becoming more important as a food item only in the 3+ to 5+ age-classes. The concentrations of methylmercury and PCBs in most of the important food items have been measured for 1973. A normalization procedure on this data was used to determine effective, seasonally invariant, C_{pf} values for each age-class. Variation of pollutant concentration in diet with age-class of fish appeared to be sufficiently small to be ignored, permitting the use of an average pollutant concentration in food of 33×10^{-9} g/g CH_3 Hg and 130×10^{-9} g/g PCBs.

Residue analyses of *Perca flavescens* (Norstrom and Peter 1973; Norstrom and Brownstein 1974) netted between October 1972 and August 1973 were used to determine values for pollutant concentration in tissues for comparison with values simulated by the bioaccumulation model.

5. *Clearance coefficient (k_{cl}) and body weight exponent (ζ) for clearance*

The values of 0.202 $g^{0.58}$ wk^{-1} for k_{cl} and -0.58 for ζ that were derived from the experimental work on methylmercury clearance from goldfish (Fig. 2) were accepted for *Perca flavescens*. The whole-body clearance half-life for 300-g *Esox lucius* from Järvenpää et al. (1970) appears to confirm that there is little species dependence for methylmercury clearance. The data of Lockhart et al. (1972) for clearance of methylmercury from *Esox lucius* transplanted from a contaminated to an uncontaminated lake are also in general agreement with our clearance parameters. Thus, if equation (14) is applied to the five fish that had cleared for 1 yr and had grown from 784 to 1670 g, the whole-body fractional clearance of 30%/yr yields values of k_{cl} from 0.33 to 0.51 $g^{0.58}$ wk^{-1}, which, considering the accuracy of the estimate, is well within the range of our value of 0.202 $g^{0.58}$ wk^{-1} given in Table 1.

No direct evidence is available for the body weight dependence of organochlorine clearance. However, information on fractional clearance can be used to determine k_{cl} if the value of ζ is assumed the same as for methylmercury as a first approximation. Hattula and Karlog (1973) presented data on PCB clearance from goldfish that can be analyzed to give a fractional clearance of 0.090 wk^{-1} for fish weighing from 0.7 to 4.6 g, corresponding to $k_{cl} = 0.07$ to 0.22 $g^{0.58}$ wk^{-1}. Because the PCB residue data and the properties of the model required the PCB clearance equation to be similar in form to that for methylmercury, and there is some evidence that fractional clearance values are much the same for both pollutants, ζ for PCB was assumed the same as for methylmercury, and k_{cl} was adjusted slightly higher to 0.238 $g^{0.58}$ wk^{-1} to achieve a better fit to the residue data.

Seasonal Variation in Temperature and Growth

River water temperatures and fish growth are by no means constant during the extreme climatic variations which occur in the Ottawa region. Seasonal variations in river water temperatures are shown in Fig. 4, along with values for low

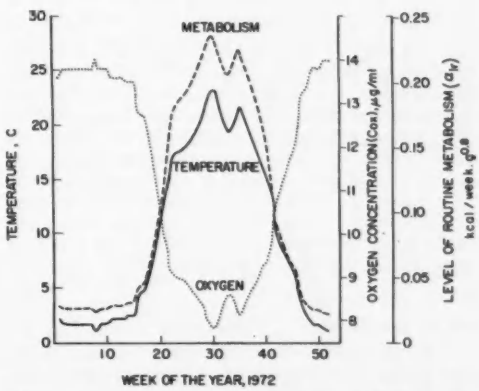

FIG. 4. Water temperature in the Ottawa River (1972) and its effect on predicted oxygen concentration and level of low routine metabolism in *Perca flavescens*. Oxygen concentration is calculated from equation (20) and level of low routine metabolism is determined from Fig. 3.

TABLE 3. Relative accuracy of various methods for determining total annual ration[a].

Age-class	True annual ration (*kcal/yr*)	Ratio of approximate to true annual ration, using:[b] α_{lr} at $\overline{T}$, W	$\bar{\alpha}_{lr}$, W	true α_{lr}, W_v	α_{lr} at $\overline{T}$, W_v	$\bar{\alpha}_{lr}$, W_v
0+	33.5	1.04	1.12	0.73	0.81	0.86
1+	106	0.97	1.06	0.81	0.83	0.90
2+	204	0.94	1.03	0.85	0.83	0.91
3+	307	0.93	1.02	0.88	0.84	0.92
4+	410	0.91	1.01	0.90	0.84	0.93
5+	498	0.91	1.01	0.92	0.85	0.95

[a]To calculate annual ration, the formula $(1/e_f)(\alpha_{lr}W^\gamma + 2d\mathrm{W}/dt)$ was integrated numerically from the 18th week (approximate hatching date) of one year to the 18th week of the next year. The true value was obtained by using weekly increments of α_{lr} and W, and the approximate values were obtained by using the α_{lr} and W combinations indicated in the table.

[b]T and α_{lr} are mean annual temperature and mean annual α_{lr} determined from the data shown in Fig. 4, and have values of 9.74 C and 0.104 kcal/wk·$g^{0.8}$, respectively. α_{lr} at T is the value of α_{lr} from Fig. 3 corresponding to T and has the value 0.091 kcal/wk·$g^{0.8}$. These values are constant with respect to season and age-class. True α_{lr} and W are the actual seasonal values, and W_v is weight modeled on an annual increment basis by the von Bertalanffy growth equation.

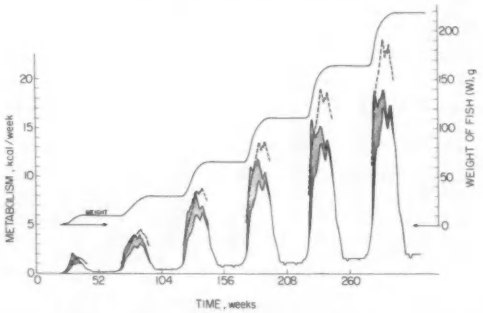

FIG. 5. Estimated growth curve (average wet weight per fish) of the *Perca flavescens* population in the Ottawa River on a weekly basis over a 6 yr growth period. In the lower set of curves, the uppermost solid line represents total metabolic rate (Q), the lower solid line is low routine metabolic rate (Q_{lr}), and the shaded area between is growth-related metabolic rate (Q_e). The dashed line represents active metabolic rate (Q_{max}). Q_{max}, Q, and Q_{lr} were estimated using the weekly growth curve, the relations shown in Fig. 3 and 4, and equation (10).

routine metabolism (α_{lr} determined from Fig. 3) and oxygen concentration in water (C_{ox}, calculated from equation (20)). Figure 5 shows the average wet weight per fish of the *Perca flavescens* population over a 6-yr growth period. The corresponding values for active metabolism (Q_{max}), total metabolism (Q) and "low routine" or maintenance metabolism (Q_{lr}) also illustrated in Fig. 5, were obtained using equation (10) with data input from temperature and growth values illustrated in Fig. 4 and 5 and the metabolism–temperature relation illustrated in Fig. 3. Total metabolism of each age-class is close to active metabolism from the 18th week (onset of growth) to the week when growth begins to decelerate, as shown by the results in Fig. 5.

The most notable feature of the metabolism curves is the large proportion of the annual metabolism (and therefore pollutant uptake) predicted to occur during the 4-mo period from May to September. Also, predicted metabolic rate exceeds active metabolism (the theoretical upper limit) to a significant extent only in the case of young fish in their first growing season.

Reliable growth rate data on a seasonal basis are difficult to obtain, compared to the relative ease of establishing estimates of annual growth. It becomes important, therefore, to determine whether or not seasonal detail in growth rate is necessary to adequately predict pollutant uptake. It would also be a useful additional simplification if constant values of low routine metabolism (α_{lr}) and dissolved oxygen concentration (C_{ox}) based on mean annual temperature, for example, could be used to predict pollutant uptake.

Estimates of the total annual ration (R_{annual}) and total annual water flow past the gills (V_{annual}) have been employed to assess the reliability of using these simplifications to the information input required by the model. Values for R_{annual} and V_{annual}, computed on the basis of equations (21) and (22), are reported in the second column of Tables 3 and 4. These values are referred to as

TABLE 4. Relative accuracy of various methods for determining total annual water flow past the gills[a].

Age-class	True annual water flow (g/yr) $\times 10^{-6}$	Ratio of approximate to true water flow, using:[b] α_{lr} at $\bar{T}$, W, C_{ox} at $\bar{T}$	$\bar{\alpha}_{lr}$, $\bar{W}$, $\bar{C}_{ox}$	true α_{lr}, W_v, true C_{ox}	α_{lr} at $\bar{T}$, W_v, C_{ox} at $\bar{T}$	$\bar{\alpha}_{lr}$, $\bar{W}_v$, $\bar{C}_{ox}$
0+	0.82	0.88	0.93	0.54	0.64	0.66
1+	2.69	0.82	0.87	0.70	0.67	0.71
2+	5.35	0.79	0.84	0.77	0.68	0.72
3+	8.25	0.78	0.83	0.82	0.70	0.74
4+	11.2	0.77	0.83	0.85	0.70	0.75
5+	13.9	0.77	0.83	0.89	0.71	0.77

[a]To calculate annual water flow, the formula $(1/e_{ox}q_{ox})(\alpha_{lr}W^{\gamma} + (dW/dt)/C_{ox})$ was integrated numerically from the 18th week (approximate hatching date) of one year to the 18th week of the next year. The true value was obtained by using weekly increments of α_{lr}, W, dW/dt and C_{ox}, and the approximate values were obtained using various estimations for these parameters as indicated in the table.

[b]T, α_{lr} and C_{ox} are mean annual temperature, mean annual α_{lr} and mean annual C_{ox} determined from the data shown in Fig. 4 to have the values 9.74 C, 0.104 kcal/wk·g$^{0.8}$, and 11.33×10^{-6} g/g, respectively. α_{lr} and C_{ox} at T are the values from Fig. 3 and equation (20) corresponding to T, and have values 0.091 kcal/wk·g$^{0.8}$ and 10.85×10^{-6} g/g, respectively. These values are constant with respect to season and age-class. True α_{lr}, true C_{ox}, and W are the actual seasonal values, and W_v is weight modeled on an annual increment basis by the von Bertalanffy growth equation. Wherever W_v is indicated, the corresponding dW_v/dt weekly increments were used in integrating the second term of the equation, $(dW/dt)/C_{ox}$.

"true" since they were calculated from seasonal growth and temperature data. Values based on various simplifications are referred to as "approximate" and are presented in Tables 3 and 4 as a fraction of the true value. For example, to assess the effect of an approximation to routine metabolism (α_{lr}), its approximate value is used in equation (21),

$$R_{annual} = \frac{1}{e_f} \times \int_0^{52} \left[\alpha_{lr} W^{\gamma} + (\beta + 1) \frac{dW}{dt} \right] dt \quad (21)$$

and equation (22),

$$V_{annual} = \frac{1}{e_{ox} q_{ox}} \int_0^{52} \left[\frac{\alpha_{lr} W^{\gamma} + \beta \frac{dW}{dt}}{C_{ox}} \right] dt \quad (22)$$

Virtually all the approximate methods underestimate R_{annual} and V_{annual}, the latter more seriously, because of the combined effect of seasonal variation on metabolism and oxygen concentration. However, none of the approximate methods is more than 30% in error. From the data in Tables 3 and 4 it would appear that the most uniformly acceptable approximate method should employ mean annual α_{lr} and C_{ox}, and seasonal growth. In the absence of information on seasonal growth, the mean annual values for α_{lr} and C_{ox} are also generally the most satisfactory approximations when used in combination with the von Bertalanffy growth equation fitted to annual growth measurements.

When information is available on seasonal growth, it should be used, but its use can be simplified by employing von Bertalanffy growth (W_v) in conjunction with $\|\alpha_{lr}\|$ and $\|C_{ox}\|$, "constant normalized" values for each age-class. The normalized values $\|\alpha_{lr}\|$ and $\|C_{ox}\|$ are defined by equations (23) and (24) so that for each age-class the values of R_{annual} and V_{annual} are equal to the "true" values.

Thus, $\|\alpha_{lr}\|$ is defined by the equation

$$\|\alpha_{lr}\| = \frac{\int_0^{52} \alpha_{lr} W^{\gamma} dt}{\int_0^{52} W_v^{\gamma} dt} \quad (23)$$

and $\|C_{ox}\|$ by the equation

$$\|C_{ox}\| = \frac{\|\alpha_{lr}\| \int_0^{52} W_v^{\gamma} dt + \beta \int_0^{52} dW}{\int_0^{52} \frac{\alpha_{lr} W^{\gamma} + \beta \frac{dW}{dt}}{C_{ox}} dt} \quad (24)$$

TABLE 5. Values for each age-class of level of low routine metabolism, α_{lr}, and concentration of oxygen in water, C_{ox}, normalized with respect to seasonal temperature and growth fluctuations, and mean annual metabolism values.

	Constant normalized values[a]		Mean annual values[b]			
Age class	$\|\|\alpha_{lr}\|\|$ ($kcal/wk \cdot g^{0.8}$)	$\|\|C_{ox}\|\|$ (g/g) $\times 10^6$	$\bar{Q}_{lr}$ ($kcal/wk$)	$\bar{Q}_c$ ($kcal/wk$)	$\bar{Q}$ ($kcal/wk$)	$\bar{Q}_c/\bar{Q}$
0+	0.136	8.95	0.34	0.15	0.49	0.31
1+	0.125	9.13	1.22	0.41	1.63	0.25
2+	0.121	9.23	2.58	0.67	3.25	0.21
3+	0.117	9.26	4.14	0.88	5.02	0.18
4+	0.115	9.33	5.85	1.02	6.87	0.15
5+	0.112	9.33	7.46	1.06	8.52	0.12

[a]The normalization procedure is given by equations (23) and (24). The integrations were carried out from the 18th week of one year to the 18th week of the next year. Constant normalized values, used in conjunction with the von Bertalanffy growth model, give the correct annual ration and water flow past the gills.

[b]Total metabolism, Q, is the sum of low routine metabolism, Q_{lr}, and growth-related metabolism, Q_c. Mean annual values were calculated using seasonal values for all parameters.

The resulting equations for ration and water flow become

$$R = \frac{1}{e_f}\left[\|\alpha_{lr}\| W_v^{\gamma} + (\beta + 1)\frac{dW_v}{dt}\right] \quad (25)$$

and

$$V = \frac{1}{e_{ox} q_{ox} \|C_{ox}\|}\left[\|\alpha_{lr}\| W_v^{\gamma} + \beta \frac{dW_v}{dt}\right] \quad (26)$$

Mean annual α_{lr} and α_{lr} at mean annual temperature are both lower than $\|\alpha_{lr}\|$ for any age-class (Table 5), the difference becoming smaller for older age-classes because $\|\alpha_{lr}\|$ decreases gradually with increasing age. Mean annual C_{ox} and C_{ox} at mean annual temperature are never more than 20% higher than $\|C_{ox}\|$, which in itself is not dependent on age-class.

The "true" mean annual values for low routine metabolism $\bar{Q}_{lr}$ and growth related metabolism $\bar{Q}_c$ are presented in Table 5. The ratio $\bar{Q}_c/(\bar{Q}_c + \bar{Q}_{lr})$ demonstrates that growth related metabolism decreases from 31% of total metabolism in the first year, to 12% in the sixth year.

From these results, it can be concluded that even when α_{lr} and C_{ox} values are normalized to give "true" estimates of ration and water flow past the gills, the use of equations (25) and (26) can be expected to cause inaccuracies in estimates of pollutant uptake. For the purposes of predicting pollutant bioaccumulation in nature, however, errors associated with the use of a continuous growth function of the von Bertalanffy type would be relatively insignificant compared to errors associated with the large and ill-defined differences in 1) growth rate between individual fish of the same age-class that occur in natural populations, and 2) seasonal variations in pollutant concentration in water and food.

Simulation of Pollutant Bioaccumulation

Parameter values in Table 1 were used to simulate the concentration of methylmercury and PCBs in body tissue as a function of body weight. The predicted tissue concentration values fall within the natural scatter of the data, as illustrated in Fig. 6. The general trend of increasing residue levels with increasing body weight, observed in the field data, is reproduced extremely well by the simulated results. The similar variation with body weight between the predicted and observed concentration values at small body weights confirms the high degree of realism of the model, since a much faster rate of increase of pollutant concentration with increasing body weight is observed in the small, faster growing fish compared to the larger fish. Although our results give us confidence in the form of the model equation (15), it should be noted that a low estimate in any coefficient of the W^{γ} and dW/dt terms could be compensated by a high estimate in another coefficient without affecting the simulated values. The estimates of pollutant related parameters (e_{pw}, C_{pw}, C_{pf}) are the ones most subject to possible error due to inadequate definition of seasonal variation.

The predicted relative importance of the water vector to the total pollutant uptake increased slightly during the 5-yr growth period, from 37 to 41% for methylmercury and from 31 to 34% for PCB. An increase is expected from the form of the bioaccumulation equation, in which decreasing growth rate with increasing weight has

TABLE 6. Sensitivity of the simulations for methylmercury bioaccumulation to changes in the concentration of methylmercury in water (C_{pw}) and food (C_{pf}), and in the clearance coefficient (k_{cl})[a].

Changes in reference simulation[b]	C_{pw} ($g/g \times 10^9$)	C_{pf} ($g/g \times 10^9$)	k_{cl} ($g^{0.58}\ wk^{-1}$)	ϵ ($g/g^{1+\delta} \times 10^9$)	υ	Percent uptake from water[c]
none	0.004	32	0.202	50.1	0.23	41
higher C_{pw}	0.008	32	0.202	74.1	0.22	58
lower C_{pw}	0.002	32	0.202	41.7	0.22	26
higher C_{pf}	0.004	64	0.202	83.2	0.22	26
lower C_{pf}	0.004	16	0.202	35.5	0.23	58
higher k_{cl}	0.004	32	0.404	30.9	0.24	40
lower k_{cl}	0.004	32	0.101	70.8	0.22	40

[a]Sensitivity is measured by changes in the empirical parameters ϵ and δ in equations (27) and (28).
[b]Parameter values for the methylmercury reference simulation are given in Tables 1 and 5. The simulations are shown in Fig. 7.
[c]Calculated at W = 150 g.

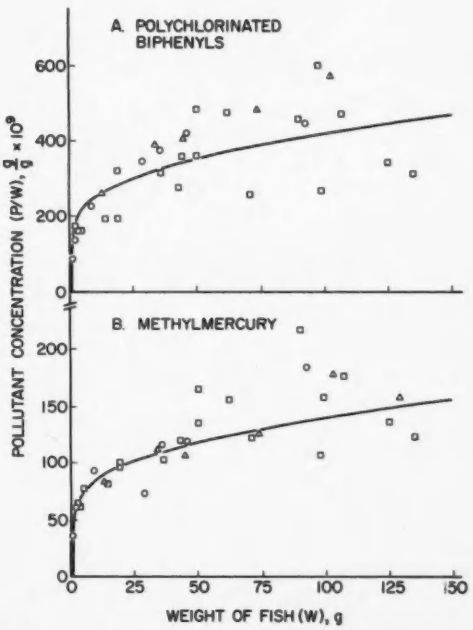

FIG. 6. Simulated tissue concentrations of A, PCB (as Aroclor 1254) and B, methylmercury in *Perca flavescens* using the parameter values of Table 1, compared with measured tissue residue levels. Solid line represents simulated residues; □ represents residues in fish captured on Oct. 4, 1972; ○ and △ represent residues in fish captured between July 18 and 30, 1973, at two sites 2.3 miles apart. Composite samples were analyzed when possible, particularly at small weights where up to 80 fish were combined for analysis. The composite samples ranged in weight ±10% around the mean. Total fish represented in the study are 137 for 1972 and 162 for 1973.

a stronger depressing effect on pollutant uptake from food than on uptake from water.

It was noted that a log/log transformation of the observed pollutant concentration vs. body weight data gave an approximately linear correlation down to weights as low as 1 g:

$$\log (P/W) = \epsilon + \upsilon \log W \qquad (27)$$

or

$$P/W = \epsilon W^{\upsilon} \qquad (28)$$

Since the simulated log (P/W) vs. log W curves were also approximately linear, the sensitivity of the simulations to changes in parameter values could be empirically measured by changes in ϵ and υ, or by a breakdown in the validity of equation (27). The sensitivity to changes in clearance coefficient and in pollutant concentration in water and food is illustrated in Fig. 7, showing the best straight line approximation to the simulations of pollutant concentrations. The values of ϵ and υ for each set of conditions are presented in Table 6. In each case, the linear relation defined by equation (27) deviates from the simulated values by no more than 5%, verifying the integrity of equation (27). Changes in pollutant clearance coefficient and concentrations of pollutants in food and water appear to have little or no effect on the slope (υ values in Table 6) of the concentration vs. body weight relation. The value of the coefficient ϵ could be approximated by 5500 C_{pw} + 1.27 C_{pf} for the first five simulations given in Table 6; that is, there was a direct proportionality between concentration of pollutant in the fish and the concentration of pollutant in water and food. The dependence of ϵ on k_{cl} was more complex.

The sensitivity of pollutant accumulation to growth rate changes at normal and faster than normal clearance was computed for both methylmercury and PCBs by changing the value of the

TABLE 7. Sensitivity of the simulations for methylmercury and PCB bioaccumulation to changes in the growth rate at two different clearance rates.[a]

Changes in reference simulation[b]	b (wk^{-1})	k_{cl} ($g^{0.58}\,wk^{-1}$)	ϵ ($g/g^{1+\vartheta} \times 10^9$)	ϑ
		Methylmercury		
none	0.0313	0.202	50.1	0.23
faster growth	0.050	0.202	46.8	0.23
faster clearance	0.0313	0.885	15.8	0.24
faster growth and clearance	0.050	0.885	18.6	0.23
		PCB		
none	0.0313	0.238	148	0.23
faster growth	0.050	0.238	148	0.22
faster clearance	0.0313	0.885	58	0.24
faster growth and clearance	0.050	0.885	69	0.22

[a]Sensitivity is measured by changes in the empirical parameters ϵ and ϑ in equations (27) and (28).

[b]Parameter values for the methylmercury and PCB reference simulations are given in Tables 1 and 5. The reference simulations are shown in Fig. 6. Faster growth results from an increase in the von Bertalanffy growth parameter b, and faster clearance from an increase in the clearance coefficient k_{cl}.

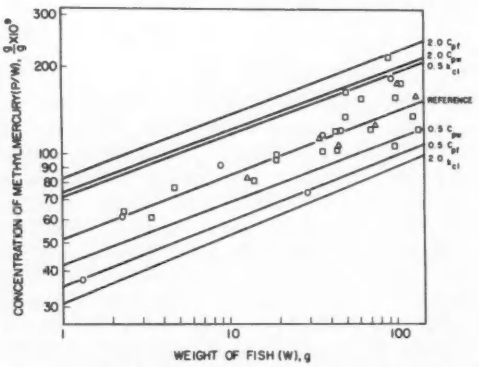

FIG. 7. Sensitivity of the simulations for methylmercury bioaccumulation to doubling and halving the values for concentration of methylmercury in water (C_{pw}) and food (C_{pf}) and the clearance coefficient (k_{cl}). See Table 6 for parameter values. Solid line represents simulated residues; ○, △, □ represent measured residue levels as defined in Fig. 6a.

parameter b in the growth equation from 0.00313 wk^{-1} to 0.005 wk^{-1}, resulting in approximately double the growth rate (146 wk to reach 150 g, rather than 248 wk). The results of the simulations are given in Table 7. At reference conditions, the time to reach a specified weight has little effect on the amount of pollutant accumulated. Methylmercury accumulation under these conditions does, however, demonstrate a slight "growth dilution" effect (deFreitas et al. 1974) due to the lower integrated metabolic rate of the fast compared to the slow growing fish in reaching a specified weight. Faster growth rates and/or slower clearance rates than those shown in Table 7 would produce a greater growth dilution effect. Other conditions that would increase the tendency for growth dilution are a lower ratio of pollutant uptake from water to pollutant uptake from food, and a higher net conversion efficiency of ingested diet to body tissue ($\beta < 1$).

At faster than reference values for clearance, the opposite to a growth dilution effect can be noted. Under these conditions of clearance, the faster the growth rate, the less time there is to clear previously accumulated pollutant, resulting in higher pollutant concentrations in tissues at any particular body weight.

The value of the body weight exponent ζ, in the clearance equation has a marked effect on pollutant accumulation. Figure 8 shows the effect of varying ζ from 0.0 (no body weight dependence) to -0.8 on the accumulation of methylmercury. A value of -0.2 for ζ corresponds to a routine metabolism dependence ($\gamma - 1$), and a value of -0.58 is the experimentally determined value for methylmercury. At weights less than 10 g, v, the slope from equation (27), is proportional to $-\zeta$. Inspection of equation (15) shows that at weights greater than 10 g, the clearance rate rapidly approaches zero for values of ζ much more negative than -1.0, and the accu-

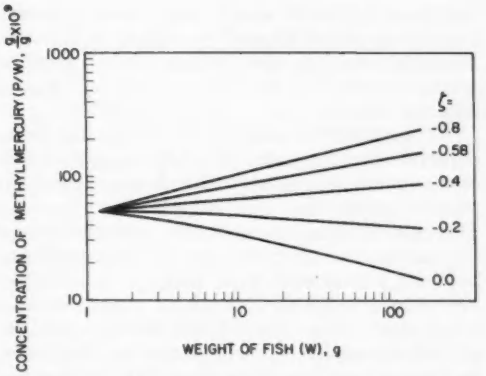

FIG. 8. Sensitivity of the simulation for methylmercury bioaccumulation to values of ζ, the body weight exponent for clearance.

mulation curve becomes dependent only on the uptake rate. The curves for all values of ζ intersect at W ≈ 1.2 g. The coefficient ϵ in equations (27) and (28) is, therefore, practically independent of ζ.

To understand further the general properties of the model it is helpful to first approximate growth rate as a parabolic function of weight. An analysis of the annual weight increment data for *Perca flavescens* by the relative standard deviation method of Parker and Larkin (1959) showed that the growth rate up to age-class 4+ could be represented by

$$dW/dt = 0.107W^{0.48} \text{ (kcal/wk)} \qquad (29)$$

Thus, from equation (10) overall metabolic rate could be described by

$$Q = 0.121W^{0.81} + 0.107W^{0.48} \qquad (30)$$

where 0.121 kcal/wk·g$^{0.81}$ is an average value for $\|\alpha_{Ir}\|$ from Table 5. The two terms in this equation are accurately represented by the single parabolic function

$$Q = 0.207W^{0.73} \text{ (kcal/wk)} \qquad (31)$$

except at very small weights. Thus, from equations (10) and (13), pollutant uptake from water is approximately proportional to W$^{0.73}$. Similarly, it can be shown from equations (11) and (12) that pollutant uptake from food is approximately proportional to W$^{0.67}$. The bioaccumulation model equation (15) can, therefore, be represented by

$$dP/dt \approx AW^{0.7\pm0.03} - k_{el}PW^{\zeta} \qquad (32)$$

where A is a constant which combines all of the coefficients in the uptake parts of the model equation.

It was found that the ratio of pollutant uptake rate to pollutant clearance rate for the simulations given in Tables 6 and 7 did not vary significantly with body weight in any given simulation, and was also independent of pollutant concentration in water and food. For example, the ratio for the first five simulations in Table 6 was 1.83 ± 0.02 for weights from 15 to 150 g. The value of the ratio did, however, depend on growth rate and clearance rate parameters. From equation (32) this result can be formulated as

$$(AW^{0.7\pm0.03}/k_{el}PW^{\zeta}) = B \qquad (33)$$

where B is constant for a fixed set of growth and clearance parameters. Thus, the concentration of pollutant at any given weight is given by

$$P/W = (A/Bk_{el})\ W^{-(0.3+\zeta)\pm0.03} \qquad (34)$$

A comparison with equation (28) shows that $\epsilon = (A/Bk_{el})$ and $\upsilon = -(0.3 + \zeta) \pm 0.03$. Therefore, for $\zeta = -0.58$, the successive approximations given by equations (29)–(34) yield a value of $\upsilon = 0.28 \pm 0.03$ compared to the value of $\upsilon = 0.22 \pm 0.01$ from the simulations summarized in Tables 6 and 7. Since equation (34) yields a reasonably accurate value of υ, and predicts that ϵ is directly proportional to the uptake parameters, but a complex function of growth and clearance parameters, it is a satisfactory explanation for the dependence of pollutant bioaccumulation on body weight empirically described by equations (27) and (28). For those simulations depicted in Fig. 8 where equation (27) was an inadequate representation over the whole weight range from 1 to 150 g, the ratio of pollutant uptake rate to clearance rate was found to vary significantly in the weight ranges where log (P/W) vs. log W was not linear.

Discussion

The approach taken in this paper to the problem of modeling pollutant bioaccumulation depends heavily on the correct use of information on fish bioenergetics. Specifically, the model must have the ability to predict the total metabolic requirements of a fish on the basis of its body size, growth rate, and environmental temperature. In addition to using parameter values derived from laboratory experiments on pollutant dynamics and bioenergetics, the present model differs in several respects from previous proposals (Fagerström and Åsell 1973; Norstrom et al. 1975).

We have proposed that the expression for total metabolism include a term dependent on growth rate as in equation (10), in which the growth rate coefficient, β, is a measure of net efficiency

of energy assimilation from the diet and net conversion efficiency of assimilated energy. On the basis of arguments presented in the section on bioenergetics, we feel that this is a realistic and necessary departure from Winberg's (1956) approach of simply doubling the value of routine metabolic rate, in agreement with the criticisms of Warren and Davis (1967).

A second and probably more important aspect of the present model is the form of the clearance function as given in equation (14), where the exponent of body weight depends on the nature of the compound and possibly the species of fish, but is not directly related to the body weight exponent for routine metabolism, γ. This resulted from a distinct lack of success in using a body weight exponent for clearance of about -0.2, corresponding to a dependence of clearance on metabolic rate (Norstrom et al. 1975), and experimental evidence on methylmercury clearance that gave a value for ζ of -0.58, independent of temperature and ration level (Sharpe et al. 1975). Clearance of some pollutants may be metabolic rate dependent, but it appears that experimental evidence is essential before any assumptions are made. Even $\zeta \approx -0.2$ does not necessarily mean that clearance is metabolic rate dependent, since the clearance constant must first be proven to vary with metabolism at a given weight.

Fagerström et al. (1974), using a body weight exponent for clearance at -0.19, reported that their computed values were above the real values for methylmercury concentration in northern pike (*E. lucius*) weighing 300 g or less. They suggested that this discrepancy resulted from not allowing the pollutant uptake parameters to vary with age, but it may equally well have resulted from an incorrect value of ζ. From an analysis of methylmercury levels in northern pike in terms of their model, Fagerström et al. (1975) deduced that either the rate of uptake of methylmercury was dependent on a power of W greater than $\gamma = 0.81$, or the rate of clearance was dependent on power of W less than $\zeta = -0.19$. Our value of $\zeta = -0.58$ is consistent with this finding.

The close fit between simulated and real residue levels of PCBs and methylmercury (Fig. 6) demonstrates that the pollutant bioaccumulation model, defined by equation (15), has been formulated with sufficient detail to have general applicability to the accumulation of a wide range of pollutants. Any further increase in detail would have to depend on the availability of species- and location-specific information on factors controlling growth rates, metabolic rates, and pollutant dynamics, information that is not generally available. For instance, it is particularly difficult to obtain a precise definition of seasonal variation in growth rate. It is important, therefore, to know how accurately and with how much resolution the data must be obtained to provide acceptable levels of confidence in the model predictions.

We have shown that, given the present level of detail in the model, it is sufficient to have annual growth data and mean annual values of routine metabolism and oxygen concentration. These approximations, applicable to slowly clearing pollutants, are more valid when applied to pollutant concentrations in tissue of fish caught just after completion of their major annual growth period than for fish that have maintained a constant weight for a long period of time, such as those captured in early spring. Despite conditions of wide temperature extremes and short growing season which exist in the Ottawa River, we obtained only a 30% error in annual ration and annual water flow past the gills using these approximations, compared to detailed seasonal information (Tables 3 and 4). Hence, the use of these approximations should have quite general applicability within defined but limited levels of confidence.

The overall form and magnitude of methylmercury accumulation by *Perca flavescens* as a function of body weight was accurately simulated at all weights using parameters determined without reference to the levels of methylmercury in the reference population of fish. In the case of PCB simulations, inadequate experimental information on clearance required "calibration" of the model by choosing a value for the clearance constant which produced a good fit to the residue data. Since choosing a body weight exponent for clearance much different from the methylmercury value ($\zeta = -0.58$) would have made the fit worse, the value of the clearance coefficient is probably correct within the limits set by confidence in the uptake parameters.

On initial inspection, the additional growth term ($d\mathrm{W}/dt$) in the expression for uptake of pollutant from food as opposed to the expression for uptake from water in equation (15) suggests that the relative magnitude of the two uptake vectors, and, therefore, the concentrations in food and water, can be established from residue levels in fish as a function of body weight. Unfortunately, this cannot be done, since the sensitivity studies shown in Fig. 7 demonstrate that the pollutant concentrations in (and efficiencies of assimilation from) food and water are quite complementary, and an increase in one can be compensated for by a decrease in the other without a significant change in the simulated pollutant concentration vs. body weight relation. It is noteworthy, however, that when either the food or

water vector is defined, equation (15) can be used to estimate the magnitude of the other vector if the clearance parameters are established as well.

The inability to differentiate between uptake vectors results from the slope v (Tables 6 and 7) of the log/log plots of concentration vs. body weight being so remarkably constant. This property is apparent in the approximation given by equation (34), which was derived from the observation that, for each simulation, predicted uptake was essentially proportional to clearance despite a wide variation in model parameters, including a doubling in growth rate. As a consequence, equation (34) suggests the possibility that residue levels in fish can be used to obtain estimates of the body weight exponent for clearance. A study of the trace element content of several molluscs as a function of body weight appears to confirm the utility of this approach (Boyden 1974). The log/log transformations of concentrations vs. body weight were linear, with slopes ranging from −0.23 to 1.0. In most cases, however, the slopes were constant for a particular species/metal combination, regardless of the environmental concentration.

There are several limitations to the interpretation of the model in terms of equation (34). It is expected that for slowly clearing pollutants such as methylmercury and PCBs with which we have dealt, the use of equation (34) will be valid provided the following conditions are met: 1) the concentration of pollutant in water and food is reasonably constant throughout the growth period being considered, and 2) growth is described by the Parker and Larkin (1959) parabolic equation (29). These conditions may not often be completely satisfied in a natural environment, since growth rate begins to decelerate in older fish, concentrations of pollutants in water may be quite seasonal, and changes in food type and size preference with age can cause changes in concentration of pollutant in food.

The ability of residue data to be correlated by a log/log transformation is not enough evidence to assume that the conditions for the validity of equation (34) have been met. Nevertheless, we feel that equation (34) may provide a worthwhile approach to the analysis of residue data when insufficient information is available to analyse the data in terms of the whole model.

Acknowledgments

We wish to acknowledge the help of Dr D. Miller, the efforts of the University of Ottawa students who captured the fish, and Drs D. Peter and M. Brownstein who performed the mercury analysis. Computer programming was done by Mrs J. M. Ridgeway.

BEAMISH, F. W. H. 1964. Respiration of fishes with special emphasis on standard oxygen consumption. II. Influence of weight and temperature on respiration of several species. Can. J. Zool. 42: 177–188.

BEAMISH, F. W. H., AND L. M. DICKIE. 1967. Metabolism and biological production in fish, p. 215–242. *In* S. D. Gerking [ed.] The biological basis of freshwater fish production. Blackwell Scientific Publications, Oxford.

BEAMISH, F. W. H., A. J. NIIMI, AND P. F. K. P. LETT. 1975. Bioenergetics of teleost fishes: Environmental influences, p. 187–209. *In* L. Bolis, H. P. Maddrell, and K. Schmidt-Nielsen [ed.] Proc. Int. Conf. on Comparative Physiology — Functional Aspects of Structural Materials, June 17–22, 1974, Ascona, Italy. North Holland Publishing Co., Amsterdam.

BERTALANFFY, L. VON. 1938. A quantitative theory of organic growth. (Inquiries on growth laws. II.) Human Biol. 10: 181–213.

BOYDEN, C. R. 1974. Trace element content and body size in molluscs. Nature 251: 311–314.

BRETT, J. R. 1965. The relation of body size to rate of oxygen consumption and sustained swimming speed of sockeye salmon (*Oncorhynchus nerka*). J. Fish. Res. Board Can. 22: 1491–1501.

BROWN, M. E. 1957. Experimental studies on growth, p. 361–400. *In* M. E. Brown [ed.] The physiology of fishes. Academic Press, Inc., New York, N.Y.

BURKETT, R. D. 1974. The influence of temperature on uptake of methylmercury-203 by bluntnose minnows, *Pimephales notatus* (Rafinesque). Bull. Environ. Contam. Toxicol. 12: 703–709.

BURROWS, W. D., AND P. A. KRENKEL. 1973. Studies on uptake and loss of methylmercury-203 by bluegills (*Lepomis macrochirus* Raf.). Environ. Sci. Technol. 7: 1127–1130.

DEFREITAS, A. S. W., M. A. J. GIDNEY, A. E. MCKINNON, AND R. J. NORSTROM. 1975. Factors affecting whole body retention of methyl mercury in fish. *In* Proc. Hanford Life Sciences Symposium on the Biological Implications of Metals in the Environment, Sept. 29–Oct. 1, 1975, Richland, Wash. Energy Res. Dev. Adm. Symp. Ser. 15. (In press)

DEFREITAS, A. S. W., AND J. S. HART. 1975. Effect of body weight on uptake of methylmercury by fish. Water Quality Parameters, ASTM STP 573, Am. Soc. Test. Mater. p. 356–363.

DEFREITAS, A. S. W., S. U. QADRI, AND B. E. CASE. 1974. Origins and fate of mercury compounds in fish, p. 31–36. *In* Proc. Int. Conf. on Transport of Persistent Chemicals in Aquatic Ecosystems, May 1–4, 1974, Ottawa, Ont.

FAGERSTRÖM, T., AND B. ÅSELL. 1973. Methyl mercury accumulation in an aquatic food chain. A model and some implications for research planning. Ambio 2: 164–171.

FAGERSTRÖM, T., B. ÅSELL, AND A. JERNELÖV. 1974. Model for accumulation of methyl mercury in northern pike, *Esox lucius*. Oikos 25: 14–20.

FAGERSTRÖM, T., R. KURTÉN, AND B. ÅSELL. 1975. Statistical parameters as criteria in model evaluation:

kinetics of mercury in pike *Esox lucius*. Oikos 26: 109–116.

FORTIN, R., AND E. MAGNIN. 1972. Croissance en longueur et en poids des perchaudes *Perca flavescens* de la Grande Anse de l'île Perrot au lac Saint-Louis. J. Fish. Res. Board Can. 29: 517–523.

FRY, F. E. J. 1957. The aquatic respiration of fish, p. 1–63. *In* M. E. Brown [ed.] The physiology of fishes. Academic Press, Inc., New York, N.Y.

GAKSTATTER, J. K., AND C. M. WEISS. 1967. The elimination of DDT-C^{14}, dieldrin-C^{14}, and lindane-C^{14} from fish following a single sublethal exposure in aquaria. Trans. Am. Fish. Soc. 96: 301–307.

HANNERZ, L. 1968. Experimental investigations on the accumulation of mercury in water organisms. Rep. Inst. Freshwater Res. Drottningholm 48: 120–176.

HATTULA, M. L., AND O. KARLOG. 1973. Absorption and elimination of polychlorinated biphenyls (PCB) in goldfish. Acta Pharmacol. Toxicol. 32: 237–245.

JÄRVENPÄÄ, A., M. TILLANDER, AND J. K. MIETTINEN. 1970. Methylmercury: half-time of elimination in flounder, pike and eel. Suom. Kemistil. B43: 439–442.

JOB, S. V. 1955. The oxygen consumption of *Salvelinus fontinalis*. Univ. Toronto Stud. Biol. Ser. No. 61. Publ. Ont. Fish. Res. Lab. 73: 39 p.

JOHNSON, L. 1966. Experimental determination of food consumption of pike, *Esox lucius*, for growth and maintenance. J. Fish. Res. Board Can. 23: 1495–1505.

KERR, S. R. 1971a. Analysis of laboratory experiments on growth efficiency of fishes. J. Fish. Res. Board Can. 28: 801–808.

1971b. Prediction of fish growth in nature. J. Fish. Res. Board Can. 28: 809–814.

KROGH, A. 1941. The comparative physiology of respiratory mechanisms. University of Pennsylvania Press, Philadelphia, Pa. 172 p.

LLOYD, R. 1961. Effect of dissolved oxygen concentration on the toxicity of several poisons to rainbow trout (*Salmo gairdneri* Richardson). J. Exp. Biol. 38: 447–455.

LOCKHART, J. F., J. F. UTHE, A. R. KENNEY, AND P. M. MEHRLE. 1972. Methylmercury in northern pike (*Esox lucius*): distribution, elimination, and some biochemical characteristics of contaminated fish. J. Fish. Res. Board Can. 29: 1519–1523.

MACEK, J. M., AND S. KORN. 1970. Significance of the food chain in DDT accumulation by fish. J. Fish. Res. Board Can. 27: 1496–1498.

MATIDA, Y., H. KUMADA, S. KIMURA, Y. SAIGA, T. NOSE, M. YOKOTE, AND H. KAWATSU. 1971. Toxicity of mercury compounds to aquatic organisms and accumulation of the compounds by the organisms. Bull. Freshwater Fish. Res. Lab. Tokyo 21: 197–225.

MOORE, W. G. 1941. Studies on the feeding habits of fishes. Ecology 22: 91–96.

MURPHY, P. G. 1970. Effects of salinity on uptake of DDT, DDE and DDD by fish. Bull. Environ. Contam. Toxicol. 5: 404–407.

MURPHY, P. G., AND J. V. MURPHY. 1971. Correlation between respiration and direct uptake of DDT in the mosquito fish *Gambusia affinis*. Bull. Environ. Contam. Toxicol. 6: 581–588.

NIIMI, A. J., AND F. W. H. BEAMISH. 1974. Bioenergetics and growth of largemouth bass (*Micropterus salmoides*) in relation to body weight and temperature. Can. J. Zool. 52: 447–456.

NORSTROM, R. J., AND M. BROWNSTEIN. 1974. Chemical analysis, 1972–1973. Report A, p. 19A1–19A50. *In* D. R. Miller [ed.] Distribution and transport of persistent chemicals in flowing water ecosystems, Report No. 2, Ottawa River Project. Div. Biol. Sci., Natl. Res. Counc. Can., Ottawa, Ont.

NORSTROM, R. J., A. E. MCKINNON, A. S. W. DEFREITAS, AND D. R. MILLER. 1975. Pathway definition of pesticide and mercury uptake by fish. Environ. Qual. Saf. 4: 811–816.

NORSTROM, R. J., AND J. D. PETER. 1973. Chemical analysis of field samples, p. 1–38. *In* J. S. Hart [ed.] Distribution and transport of persistent chemicals in flowing water ecosystems, Interim Report No. 1, Ottawa River Project. Div. Biol. Sci., Natl. Res. Counc. Can., Ottawa, Ont.

PALOHEIMO, J. E., AND L. M. DICKIE. 1965. Food and growth of fishes. I. A growth curve derived from experimental data. J. Fish. Res. Board Can. 22: 521–542.

1966a. Food and growth of fishes. II. Effects of food and temperature on the relation between metabolism and body weight. J. Fish. Res. Board Can. 23: 869–908.

1966b. Food and growth of fishes. III. Relations among food, body size, and growth efficiency. J. Fish. Res. Board Can. 23: 1209–1248.

PARKER, R. P., AND P. A. LARKIN. 1959. A concept of growth in fishes. J. Fish. Res. Board Can. 16: 721–745.

PREMDAS, F. H., AND J. M. ANDERSON. 1963. The uptake and detoxification of C^{14}-labelled DDT in Atlantic salmon, *Salmo salar*. J. Fish. Res. Board Can. 20: 827–837.

QADRI, S. U., AND P. J. RUBEC. 1974. Age, growth and population density of brown bullhead, northern pike, walleye, sauger and yellow perch in a 3 mile section of the Ottawa River, p. 16.1–16.60. *In* D. R. Miller [ed.]. Distribution and transport of persistent chemicals in flowing water ecosystems, Report No. 2, Ottawa River Project. Div. Biol. Sci., Natl. Res. Counc. Can., Ottawa, Ont.

REED, J. K. 1969. Interaction of pesticide pollutant and aquatic food-chain organisms. Water Resour. Res. Inst., Clemson Univ., Clemson, S.C. Rep. 13: 14 p.

REINERT, R. E., L. J. STONE, AND W. A. WILLFORD. 1974. Effect of temperature on accumulation of methylmercuric chloride and p, p'-DDT by rainbow trout (*Salmo gairdneri*). J. Fish. Res. Board Can. 31: 1649–1652.

ROBINSON, J. 1967. Dynamics of organochlorine insecticides in vertebrates and ecosystems. Nature 215: 33–35.

SCOTT, W. B., AND E. J. CROSSMAN. 1973. Freshwater fishes of Canada. Bull. Fish. Res. Board Can. 184: 755–761.

SHARPE, M. A., A. E. MCKINNON, AND A. S. W. DEFREITAS. 1975. The effect of body weight on clearance of methyl mercury in the goldfish, *Carassius auratus*. Abstracts of Int. Conf. on Heavy Metals in the Environment, Oct. 27–31, 1975, Toronto, Ont. p. C26–C28.

SÖDERGREN, A. 1973. Transport, distribution, and degradation of chlorinated hydrocarbon residues in aquatic model ecosystems. Oikos 24: 30–41.

SOLOMON, D. J., AND A. E. BRAFIELD. 1972. The energetics of feeding, metabolism and growth of perch (*Perca fluviatilis* L.). J. Anim. Ecol. 41: 699–718.

SUZUKI, T., AND M. HATANAKA. 1975. Experimental in-

vestigations on the biological concentration of Mercury-II on the origin of mercury found in the body of young yellowtail. Bull. Jap. Soc. Sci. Fish. 41: 228–231.

WARREN, C. E., AND G. E. DAVIS. 1967. Laboratory studies on the feeding, bioenergetics, and growth of fish, p. 175–214. *In* S. D. Gerking [ed.] The biological basis of freshwater fish production. Blackwell Scientific Publications, Oxford.

WINBERG, G. G. 1956. Rate of metabolism and food requirements of fishes. Nauchn. Tr. Beloruss. Gos. Univ. V. I. Lenina, Minsk, 253 p. (Transl. from Russian by Fish. Res. Board Can. Transl. Ser. No. 194, 1960.) (1)

Glossary

Symbol	Unit	Description
Q_s	$kcal \cdot wk^{-1}$	standard metabolic rate
α_s	$kcal \cdot wk^{-1} g^{-\gamma}$	level of standard metabolism, Q_s/W^γ
Q_{max}	$kcal \cdot wk^{-1}$	maximum (active) metabolic rate
α_{max}	$kcal \cdot wk^{-1} g^{-\gamma}$	level of active metabolism, Q_{max}/W^γ
Q_a	$kcal \cdot wk^{-1}$	activity-related metabolic rate
Q_r	$kcal \cdot wk^{-1}$	routine metabolic rate
Q_{lr}	$kcal \cdot wk^{-1}$	low routine metabolic rate, equivalent to a maintenance ration, $Q_s + Q_a$
α_{lr}	$kcal \cdot wk^{-1} g^{-\gamma}$	level of low routine metabolism, Q_{lr}/W^γ
$\|\|\alpha_{lr}\|\|$	$kcal \cdot wk^{-1} g^{-\gamma}$	level of low routine metabolism normalized over the year for each age-class to remove the effect of temperature variations and discontinuous growth
Q_c	$kcal \cdot wk^{-1}$	metabolic rate associated with growth
β	—	coefficient relating growth rate to energy associated with growth, $Q_c/(dW/dt)$
Q	$kcal \cdot wk^{-1}$	total metabolic rate, $Q_{lr} + Q_c$
γ	—	exponent of body weight for standard, routine and active metabolic rate
W	g or kcal	wet weight of fish, and weight as a function of time on a weekly basis
dW/dt	$kcal \cdot wk^{-1}$	growth rate of fish on a weekly basis
W_v	g or kcal	wet weight of fish described as a function of time by the von Bertalanffy equation
dW_v/dt	$kcal \cdot wk^{-1}$	growth rate of fish described by the von Bertalanffy equation
L	mm	length of fish
λ	$g \cdot mm^{-\eta}$	parameters in the length–weight relation: $W = \lambda L^\eta$
η	—	
a	mm	parameters in the von Bertalanffy growth equation: $L = a\{1 - e^{-b(t-c)}\}$
b	wk^{-1}	
c	wk	
R	$kcal \cdot wk^{-1}$	ration, rate of food consumption
R_{maint}	$kcal \cdot wk^{-1}$	maintenance ration, Q_{lr}/e_f
R_{annual}	$kcal \cdot yr^{-1}$	annual ration for an age-class
e_f	—	efficiency of assimilation of metabolizable energy from food
E_g	—	gross conversion efficiency of food to body substance
E_n	—	net conversion efficiency of food to body substance, $(dW/dt)/(R - R_{maint})$
V	$g \cdot wk^{-1}$	rate of water flow past the gills
V_{annual}	$g \cdot yr^{-1}$	annual water flow past the gills for an age-class
C_{ox}	$g \cdot g^{-1}$	concentration of oxygen in water
$\|\|C_{ox}\|\|$	$g \cdot g^{-1}$	concentration of oxygen in water normalized over the year for each age-class at weekly intervals to remove the effect of temperature variations and discontinuous growth
e_{ox}	—	efficiency of assimilation of oxygen from the water by the gills
q_{ox}	$kcal \cdot g^{-1}$	caloric equivalent of oxygen
P	g	body burden of pollutant in the fish
P/W	$g \cdot g^{-1}$	concentration of pollutant in fish
dP/dt	$g \cdot wk^{-1}$	rate of change of pollutant body burden in fish
$(dP/dt)_f$	$g \cdot wk^{-1}$	rate of uptake by the fish of pollutant from food
e_{pf}	—	efficiency of assimilation of pollutant from food
C_{pf}	$g \cdot g^{-1}$	concentration of pollutant in food
$(dP/dt)_w$	$g \cdot wk^{-1}$	rate of uptake by the fish of pollutant from water
e_{pw}	—	efficiency of assimilation of pollutant from water by the gills
C_{pw}	$g \cdot g^{-1}$	concentration of pollutant in water
$(dP/dt)_{cl}$	$g \cdot wk^{-1}$	rate of clearance of pollutant from the fish
k_{cl}	$g^{-\zeta} \cdot wk^{-1}$	clearance coefficient, coefficient of body weight in the clearance expression
ζ	—	exponent of body weight in the clearance expression
ϵ	$g \cdot g^{-1-\vartheta}$	parameters in the empirical equation describing pollutant concentration in fish as a function of body weight: $P/W = \epsilon W^\vartheta$
ϑ	—	

δ-Amino Levulinic Acid Dehydratase Activity of Fish Blood as an Indicator of a Harmful Exposure to Lead

PETER V. HODSON

Department of the Environment, Fisheries and Marine Service, Canada Centre for Inland Waters, Great Lakes Biolimnology Laboratory, Burlington, Ont. L7R 4A6

HODSON, P. V. 1976. δ-amino levulinic acid dehydratase activity of fish blood as an indicator of a harmful exposure to lead. J. Fish. Res. Board Can. 33: 268–271.

The activity of red cell δ-amino levulinic acid dehydratase of rainbow trout (*Salmo gairdneri*) was depressed after exposure of the fish to lead. Concentrations of lead in water as low as 13 μg/liter caused a significant inhibition of activity after only 4-wk exposure. Assays of this enzyme's activity may provide a short-term indication of long-term harmful effects of lead.

HODSON, P. V. 1976. δ-amino levulinic acid dehydratase activity of fish blood as an indicator of a harmful exposure to lead. J. Fish. Res. Board Can. 33: 268–271.

L'exposition de truites arc-en-ciel (*Salmo gairdneri*) au plomb entraîne une diminution d'activité de la δ-amino lévulinique acide déshydratase dans les globules rouges du sang des poissons. Des teneurs en plomb dans l'eau aussi faibles que 13 μg/litre produisent une inhibition significative d'activité après exposition de 4 semaines seulement. Des essais biologiques sur l'activité de cet enzyme peuvent donner une indication à court terme des effets toxiques à long terme du plomb.

Received August 25, 1975
Accepted October 23, 1975

Reçu le 25 août 1975
Accepté le 23 octobre 1975

WATER quality criteria for heavy metals are often based on the response of fish to long-term metal exposures (NAS 1974). However, studies of these responses may take several years and provide information on only one metal and one species of fish in one situation. For example, Davies and Everhart (1973) demonstrated that low concentrations of lead in water caused black tails and spinal curvature of rainbow trout (*Salmo gairdneri*) in very hard and very soft water. This study required 1½ generations of trout exposed over 1½ yr. Therefore, a short-term indicator of sublethal lead toxicity would provide a faster, more economical way of extending these results to other fish or other situations.

The activity of δ-amino levulinic acid dehydratase (ALA-D) in blood of humans is depressed by the presence of lead in the blood. The enzyme catalyzes the formation of one molecule of porphobilinogen from two molecules of amino levulinic acid (Schalm et al. 1975). It is so sensitive to inhibition by lead that it can be used to detect a harmful exposure to lead long before toxic symptoms appear (Secchi et al. 1974).

Therefore, the activity of δ-amino levulinic acid dehydratase in blood of lead exposed and unexposed fish was measured to determine whether this is a useful technique for quick identification of harmful lead exposures.

Materials and methods — Rainbow trout (*Salmo gairdneri*) were exposed in groups of 23 to nominal lead concentrations of 0, 10, 18, 32, 56, and 100 μg/liter. There were a total of five groups and 115 fish at each concentration. The means, ±1 SD, of the chemical characteristics of the water during the exposure were as follows:

temperature	:	11 ± 0.9 C	(N = 59)
alkalinity	:	90 ± 4 mg/liter	(N = 34)
hardness	:	135 ± 2 mg/liter	(N = 35)
conductivity	:	241 ± 9 μohm/cm²	(N = 90)
pH	:	7.7 ± 0.2	(N = 81)
oxygen	:	9.8 ± 0.9 mg/liter	(N = 85)

Once each day, fish were fed to satiation with a dry, pelletized food and tanks were cleaned shortly after.

Lead, as lead nitrate, was added to the water by a toxicant doser described by Hodson (1974). The

Printed in Canada (J3958)
Imprimé au Canada (J3958)

dilution series was achieved by a proportional diluter modified from Mount and Brungs (1967). The flow rate was 2.5 liter of toxicant every 1½ min for each concentration. This flow was divided among five tanks per concentration and gave about 2.5 liter/g of fish per day. Daily lead analyses by atomic absorption spectroscopy gave actual exposure concentrations.

Blood was assayed for ALA-D activity by a method modified from Granick et al. (1972). One fish was removed from each tank at 1, 2, 4, 8, and 16 wk from the start of the lead exposure. The order in which the tanks were sampled was randomized. The tail of each fish was severed and two samples of 75 μl of blood were collected from the caudal artery with chilled, heparinized capillary tubes. One tube was capped and centrifuged to measure the microhematocrit. Blood from the second tube was immediately transferred to parafilm and 20-μl aliquots were added to each of three disposable centrifuge tubes at 11 C. The first was a blank and contained 100 μl of 0.2% Triton X-100 in 0.1 M, pH 6.2 phosphate buffer. The second and third tubes were duplicate tests and contained 100 μl of 0.2% Triton X-100 and 670 μg/ml of amino levulinic acid in 0.1 M, pH 6.2 phosphate buffer.

The tubes were capped and the samples mixed and incubated at 11 C for 2 h. The reaction was stopped with 300 μl of an aqueous solution of 4.0 g of trichloroacetic acid and 2.7 g of mercuric chloride per 100 ml. Each tube was centrifuged at 2500 × *g* for 5 min and 350 μl of supernatant was transferred to a glass test tube. The amount of porphobilinogen produced in the reaction was measured by adding 300 μl of modified Ehrlich's reagent to each test tube. This reagent consisted of 168 ml glacial acetic acid, 40 ml of 70% perchloric acid, 4.0 g of p-dimethyl amino benzaldehyde, 0.7 g mercuric chloride, and 12 ml distilled water. The reagent was made up immediately prior to each use.

After 15 min of color development, absorbance of each test solution was read against the appropriate blank at 553 mμ using a spectrophotometer with microcuvettes. ALA-D activity, expressed as units per milliliter of red blood cells per hour, was given by the formula:

$$\text{Activity} = \frac{D \times A}{T \times H}$$

where D = dilution coefficient = 50
A = absorbance after 2 h (avg of two determinations)
T = incubation time (2 h)
H = hematocrit ÷ 100

The mean of all control results was regarded as 100% of activity and all results were expressed as a proportion of the control mean activity for each sample day. The purpose of this transformation was to remove week to week variability introduced by using a fresh solution of Ehrlich's reagent for each sampling day.

Results were analyzed by a split-plot analysis of variance (Steel and Torrie 1960) where lead concentrations were whole plots and sample times were split plots.

Results and discussion — Actual lead concentrations in exposure tanks were higher than nominal concentrations:

Expected concn (μg/liter)	Measured concn ($\bar{x}$) (μg/liter)	No.	SD (μg/liter)
Control	3	130	3
10	13	130	4
18	23	129	7
32	38	133	9
56	66	128	14
100	143	129	45

The deviations from expected values were slightly less if the background lead in control water is subtracted. All subsequent results are compared to actual concentrations.

Two hours of ALA-D activity in test solutions produced enough porphobilinogen for absorbance readings ranging from 0.04 to 0.34. Most readings were between 0.1 and 0.2. Enzyme activity, calculated by the formula, ranged from 3.6 to 26.4 U/ml of red blood cells per hour. Activity of blood from control fish was usually greater than 20 U/ml of red blood cells per hour while that from exposed fish was less. When absolute values were transformed to a percentage of mean control concentrations, values ranged from 18 to 160%.

Figure 1 demonstrates how ALA-D activity of blood varied with lead concentration and exposure time. As lead concentrations increased, the degree of enzyme inhibition, relative to controls, increased. Similarily, at any given lead concentration, an increasing duration of exposure caused an increasing inhibition.

The shaded band for Fig. 1 indicates the minimum significant difference between tests and controls as measured by Duncan's New Multiple Range Test (Steel and Torrie 1960). Enzyme activity in blood of fish exposed to 143, 66, and 38 μg/liter lead differed significantly from control activity after only 1 wk. At 143 μg/liter, activity was 50% of control values after only 1 wk, and by 16 wk, it had declined to 26%. At 23 μg/liter, activity dropped sharply after 2 wk but returned to control value by 4 wk. Activity was consistently different from control values only after 8 wk. The lowest lead concentration, 13 μg/liter, caused a nonsignificant depression of activity during the first 2 wk. After 4 wk, activity was significantly lower than control activity by a small margin, and by 16 wk, it was depressed to 60% of control values.

These results are in contrast to those of Jackim (1973). He observed inhibition of liver ALA-D

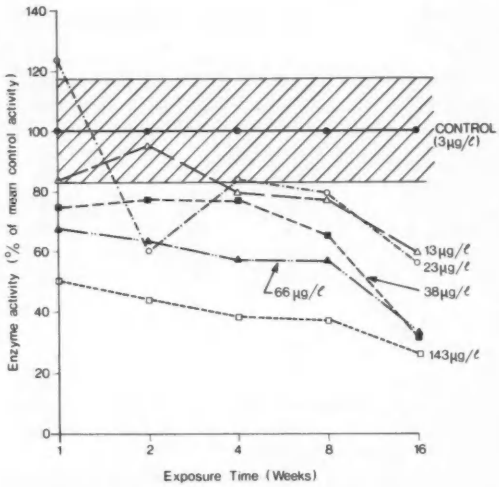

FIG. 1. Inhibition of rainbow trout (*Salmo gairdneri*) δ-amino levulinic acid dehydratase activity by exposure to lead. The shaded area represents the minimum significant difference from control values. The numbers to the right are the lead concentrations in water.

activity of mummichog (*Fundulus heteroclitus*) only after 4 wk exposure to lead concentrations of 10–50 mg/liter. These concentrations are about 1000 times greater than those observed to be effective in this experiment. Possible reasons are that he used a static exposure system and saline water, so that lead concentrations declined with time. We have found that ALA-D activity of liver and kidney is quite low so that changes in activity may be more difficult to detect. Finally, Jackim (1973) acclimated his fish to 20 C and assayed ALA-D activity at 35 C. This large temperature difference may have changed the response of ALA-D to lead.

Therefore, in fish, activity of red blood cell ALA-D is depressed by exposure to lead in the water, the effect increasing both with lead concentration and exposure time. If ALA-D activity is an index of a lead exposure harmful to rainbow trout, the data suggests that even 13 µg/liter may be harmful. Since the next lowest concentration was 3 µg/liter, the control, harmful effects may also occur between 3 and 13 µg/liter lead.

Davies and Everhart (1973) measured chronic toxicity of lead to rainbow trout in soft and hard water. In soft water (26 mg/liter alkalinity) the maximum acceptable toxicant concentration (MATC) was 6.0–11.9 µg/liter lead. In hard water (243 mg/liter alkalinity), the MATC was 120–360 µg/liter expressed as total lead, or 18–32 µg/liter expressed as free lead. Extrapolating from these results, the MATC for free lead at an alkalinity of 90 mg/liter is about 8–14 µg/liter.

In this experiment, I observed no accumulation over time of precipitated lead as I have seen using higher lead concentrations. Therefore, I have assumed that all lead is in the free or dissolved form. ALA-D inhibition, relative to controls, predicts an MATC of 3–13 µg/liter for free lead. Since this range overlaps the range extrapolated from Davies and Everhart's (1973) work, the measurement of enzyme activity appears to provide the same prediction of safe concentrations.

The measurement of ALA-D activity in fish blood will have several advantages over life cycle experiments. The most striking of these is speed. The prediction of an MATC for lead using enzyme activity required only 16 wk of lead exposure as compared to 1½ yr for Davies and Everhart's (1973) study. While the experiments of Davies and Everhart (1973) are required for the initial MATC determination, subsequent experiments to derive MATC's for different waters and species could be based on the faster enzyme assay described above.

This experiment is a preliminary evaluation of the usefulness of δ-amino levulinic acid dehydratase in fish. Further experiments are underway to measure the response to lead of the enzyme from other species, the effect on enzyme activity of other metals and some biochemical characteristics of the enzyme.

Acknowledgments — I thank B. Blunt and A. Sippel for their extensive effort in maintaining the continuous lead exposure. The Water Quality Branch of the Inland Waters Directorate, Canada Centre for Inland Waters conducted the chemical analyses of water.

DAVIES, P. H., AND W. H. EVERHART. 1973. Effects of chemical variations in aquatic environments: Vol. III. Lead Toxicity to rainbow trout and testing application factor concept. Ecol. Res. Ser., Environ. Prot. Agency, Washington, D.C. EPA-R3-73-011C: 80 p.

GRANICK, S., S. SASSA, J. L. GRANICK, R. D. LEVERE, AND A. KAPPAS. 1972. Assays for porphyrins, δ-amino levulinic acid dehydratase, and porphyrinogen synthetase in microliter samples of whole blood: Applications to metabolic defects involving the heme pathway. Proc. Natl. Acad. Sci. U.S.A. 69: 2381–2385.

HODSON, P. V. 1974. The effect of temperature on the toxicity of zinc to fish of the genus *Salmo*. Ph.D. Thesis. Dep. Zoology, Univ. Guelph, Guelph, Ont. 189 p.

JACKIM, E. 1973. Influence of lead and other metals on fish δ-amino levulinate dehydrase activity. J. Fish. Res. Board Can. 30: 560–562.

MOUNT, D. I., AND W. A. BRUNGS. 1967. A simplified dosing apparatus for fish toxicology studies. Water Res. 1: 21–29.

NAS, 1974. Water quality criteria. 1972. Natl. Acad. Sci., Natl. Acad. Eng., Washington, D.C. USA. EPA.R3. 73-033: 594 p.

SCHALM, O. W., N. C. JAIN, AND E. J. CARROLL. 1975. Veterinary hematology. 3rd ed. Lea and Febiger, Philadelphia, Pa. 807 p.

SECCHI, G. C., L. ERBA, AND G. CAMBIAGHI. 1974. Delta-aminolevulinic acid dehydratase activity of erythrocytes and liver tissue in man. Arch. Environ. Health 28: 130–132.

STEEL, R. G. D., AND J. H. TORRIE. 1960. Principles and procedures of statistics. McGraw-Hill Book Company, Inc., New York, Toronto, and London. 481 p.

Metazoan Parasites of Arctic Char (*Salvelinus alpinus*) from the North Slope of Canada and Alaska

DWIGHT R. MUDRY[1]

Department of Biology, University of Calgary, Calgary, Alta.

AND PETER J. MCCART

Aquatic Environments Limited, Calgary, Alta. T2E 6M9

MUDRY, D. R., AND P. J. MCCART. 1976. Metazoan parasites of Arctic char (*Salvelinus alpinus*) from the north slope of Canada and Alaska. J. Fish. Res. Board Can. 33: 271–275.

Fourteen species of metazoan parasites were recovered from a total of 128 *Salvelinus alpinus* from the north slope of Canada and Alaska collected between March 31, 1971 and November 5, 1972. The parasites consisted of one monogean, four digeneans, four cestodes, two nematodes, one acanthocephalan, and two copepods. Of the parasites recovered, one was described as a new species (*Bulbodacnitis alpinus* Mudry and McCart, 1974) and three others are new North American host records (*Tetraonchus alaskensis*, *Cystidicola stigmatura*, and *Cyanthocephalus truncatus*). All of the localities sampled during this study are range extensions of the parasites found.

MUDRY, D. R., AND P. J. MCCART. 1976. Metazoan parasites of Arctic char (*Salvelinus alpinus*) from the north slope of Canada and Alaska. J. Fish. Res. Board Can. 33: 271–275.

Les auteurs ont trouvé 14 espèces de métazoaires parasites chez un total de 128 *Salvelinus alpinus* capturés sur le versant nord du Canada et de l'Alaska entre le 31 mars 1971 et le 5 novembre 1972. Ces parasites comprennent un monogénien, quatre digéniens, quatre cestodes, deux nématodes, un acanthocéphale et deux copépodes. Parmi les parasites trouvés, un est décrit comme espèce nouvelle (*Bulbodacnitis alpinus* Mudry et McCart 1974) et trois autres sont signalés pour la première fois dans cet hôte en Amérique du Nord (*Tetraonchus alaskensis*, *Cystidicola stigmatura* et *Cyanthocephalus truncatus*). Toutes les localités échantillonnées au cours de cette étude représentent une extension d'aire pour ces parasites.

Received July 27, 1975
Accepted October 17, 1975

Reçu le 27 juillet 1975
Accepté le 17 octobre 1975

INFORMATION on parasites of North American Arctic char (*Salvelinus alpinus*) is restricted mainly to reports from eastern Canada (Hicks and Threlfall 1973; Hanek and Molnar 1974). Recent activity in western arctic regions has prompted extensive investigations on the biology of *S. alpinus* which is one of the most abundant fish species along the arctic coast (see McCart and Bain 1974).

McCart and Craig (1971) described two types of Arctic char in the Sagavanirktok River, Alaska. One type, predominantly anadromous and stream-dwelling, has lower pyloric caeca and gillraker

[1]Present address: Bio-systems Consultants, Calgary, Alta. T2N 3B7.

Printed in Canada (J3927)
Imprimé au Canada (J3927)

counts than the other which appears to be entirely freshwater resident and, except for short excursions into the tributary streams, confined to lakes. The first type corresponds to the western arctic–Bering Sea form of Arctic char described by McPhail (1961), and the second type to his eastern arctic form. In this paper, the terms western form and eastern form have been used to designate stocks, within the geographic area encompassed by this study, which correspond meristically to McPhail's original descriptions. The systematic status of the two forms has not been finally resolved but it is likely that they constitute two distinct species.

The present paper is a report of the metazoan parasites of both forms of Arctic char from the north slope of Canada and Alaska.

Materials and methods — A total of 128 *S. alpinus* were examined from collections made between March 31, 1971 and November 5, 1972. Collections were made at eleven sites (see Table 1) which included samples of both lake and stream populations, freshwater-resident and anadromous populations, and populations of both the eastern and western arctic forms of the Arctic char. McCart and Craig (1971) discuss the taxonomy of Arctic char in the study area.

Hosts were collected by angling or hand seine, frozen, and transported to the University of Calgary for examination. During examination, host weight, fork length, and meristic data were recorded. The following tissues, organs, and cavities were examined and dissected when necessary: external body surface, fins, body musculature, eyes, nasal cavities, buccal cavity, gills, heart, esophagus, stomach, pyloric caeca, intestine, coelom, mesenteries, gall bladder, liver, swim bladder, kidneys, urinary duct, and gonads.

Parasites obtained were fixed in alcohol–formalin–acetic acid (AFA). Nematodes were transferred to glycerine–alcohol for clearing, and all other parasites were transferred to 70% ethanol for preservation. For identification, nematodes were examined in temporary glycerine whole mounts. Representative specimens of other helminths were stained with Grenacher's borax carmine, Celestine Blue B, or hematoxylin, and mounted in Canada balsam. Dissection of the copepods was necessary for examination of the smaller appendages. The latter were mounted temporarily in glycerine.

Results and discussion — The metazoan parasites of Arctic char collected in the study area consisted of one monogean, four digeneans, four cestodes, two nematodes, one acanthocephalan, and two copepods. Data on localities, hosts, and parasites collected are summarized in Table 1. Of the parasites recovered, one was described as a new species (*Bulbodacnitis alpinus* Mudry and McCart, 1974) and three others are new North American host records (*Tetraonchus alaskensis*, *Cystidicola stigmatura*, and *Cyathocephalus truncatus*). All of the localities sampled during the present study are range extensions of the parasites found since there are no previous reports of fish parasites from the study area.

The following parasites were recovered from the *S. alpinus* examined:

Monogenea

Tetraonchus alaskensis Price, 1937

The finding of *T. alaskensis* represents the first report of a monogenean from *S. alpinus* in North America. Bychowsky (1957) considers species of *Tetraonchus* to have a high degree of specificity for salmonids and *T. alaskensis* is known from Arctic char in the Soviet arctic (Bykhovskaya-Pavlovskaya 1962).

Digenea

Brachyphallus crenatus (Rud., 1802)

This marine hemiurid was found in small numbers in migrant *S. alpinus*. Hicks and Threlfall (1973) have reported *B. crenatus* in *S. alpinus* from Labrador.

Crepidostomum farionis (Müller, 1784)

This digenean was collected from hosts in two lake localities. *Crepidostomum farionis* has been reported in *S. alpinus* from Labrador (Hicks and Threlfall 1973).

Bunodera luciopercae (Müller, 1776)

This small digenean was collected in large numbers from hosts in three lake localities, and a single specimen was found in a fish from "Kavik Tributary." This parasite has been reported from *S. alpinus* in Labrador (Hicks and Threlfall 1973).

Phyllodistomum sp.

All four *S. alpinus* examined from "Campsite Lake" were infected with large numbers of *Phyllodistomum*. Hicks and Threlfall (1973) have reported *P. limnosa* from *S. alpinus* in Labrador.

Cestoda

Cyathocephalus truncatus (Pallas, 1781)

Cyathocephalus truncatus was collected in small numbers from fish at one stream and two lake localities. Wardle (1932) reported *C. truncatus*

TABLE 1. Localities, incidence, and intensity of helminth and arthropod parasites collected from *Salvelinus alpinus* in Yukon Territory and Alaska.

Locality and parasite	Number of fish infected/ examined	Infection intensity range (mean)	Infection site	Host life history type[a]	
Porcupine Lake, Alaska (68°47′N, 146°30′W)				FWR	Eastern
Crepidostomum farionis	4/7	1–2 (1.2)	Intestine		
Bunodera luciopercae	7/7	107–289 (196)	Intestine		
Cyathocephalus truncatus	4/7	1–34 (13)	Pyloric caeca		
Metchinorhynchus salmonis	7/7	31–95 (60)	Intestine		
"Campsite Lake", Alaska (Unnamed headwater lake, 68°36′N, 149°06′W)				FWR	Eastern
Phyllodistomum sp.	4/4	22–71 (54)	Kidney		
Eubothrium sp.	3/4	1 (1)	Pyloric caeca		
"Big Lake", Alaska (Unnamed headwater lake, 68°49′N, 145°47′W)				FWR	Eastern
Bunodera luciopercae	5/12	2–27 (10)	Intestine		
Proteocephalus sp.	9/12	2–98 (18)	Pyloric caeca		
Unnamed Lake on tributary to Canning River, Alaska (69°26′N, 146°00′W)				FWR	Western
Crepidostomum farionis	4/5	9–33 (19)	Intestine		
Bunodera luciopercae	4/5	38–163 (128)	Intestine		
Cyathocephalus truncatus	3/5	2–3 (2.3)	Pyloric caeca		
Shublik Spring, Alaska (69°27′N, 146°11′W)				FWR	Western
Bulbodacnitis alpinus	12/12	1–23 (6.4)	Pyloric caeca		
Babbage River, Yukon (68°38′N, 139°20′W)				FWR	Western
Tetraonchus alaskensis	3/29	1–2 (1.3)	Gills		
Bulbodacnitis alpinus	19/29	1–75 (13)	Pyloric caeca		
Salmincola edwardsii	2/29	1–2 (1.5)	Gills		
Joe Creek, Yukon (68°53′N, 140°59′W)				ANAD	Western
Tetraonchus alaskensis	3/41	1–4 (2.3)	Gills		
Brachyphallus crenatus	4/41	1–2 (1.7)	Intestine		
Cyathocephalus truncatus	2/41	1 (1)	Pyloric caeca		
Proteocephalus sp.	5/41	1–3 (1.6)	Pyloric caeca		
Bulbodacnitis alpinus	27/41	1–132 (24)	Pyloric caeca		
Cystidicola stigmatura	25/41	1–410 (63)	Swim bladder		
Salmincola edwardsii	2/41	1–2 (1.5)	Gills		
Salmincola carpionis	5/41	1 (1)	Gills		
Upper Firth Delta, Yukon (69°28′N, 139°30′W)				ANAD	Western
Tetraonchus alaskensis	1/13	23 (23)	Gills		
Brachyphallus crenatus	1/13	2 (2)	Intestine		
Salmincola edwardsii	1/13	1 (1)	Gills		
"Kavik Tributary", Alaska (69°37′N, 137°03′W)				ANAD	Western
Bunodera luciopercae	1/3	1 (1)	Intestine		
Bothrimonus sturionis	1/3	6 (6)	Pyloric caeca		
Proteocephalus sp.	1/3	4 (4)	Pyloric caeca		
Bulbodacnitis alpinus	1/3	38 (38)	Pyloric caeca		
Salmincola edwardsii	1/3	1 (1)	Gills		
Shaviovik River, Alaska (69°49′N, 147°37′W)				ANAD	Western
Proteocephalus sp.	1/1	5 (5)	Pyloric caeca		
Cystidicola stigmatura	1/1	3 (3)	Swim bladder		
Salmincola edwardsii	1/1	11 (11)	Gills		
Salmincola carpionis	1/1	2 (2)	Gills		
Echooka Springs, Alaska (69°16′N, 147°27′W)				ANAD	Western
Bulbodacnitis alpinus	1/1	159 (159)	Pyloric caeca		

[a]FWR, freshwater resident population; ANAD, anadromous population.

from "*S. alpinus malma*" from Spray Lakes, Alberta, an area outside of the geographic distribution of *S. alpinus* (Scott and Crossman 1973). The host reported by Wardle (1932) no doubt refers to Dolly Varden (*S. malma*) which is now considered a distinct species (Scott and Crossman 1973).

Bothrimonus sturionis Duvernoy, 1842

Six specimens of *B. sturionis* were recovered from a single fish from "Kavik Tributary." In a review of the biology of *B. sturionis*, Sandeman and Burt (1972) noted that this parasite is "littoral-estuarine" in distribution with no clear records from fish taken from the coast. The presumed short life span of *B. sturionis* (see Sandeman and Burt 1972) indicates that the host had recently arrived at the capture site on the "Kavik Tributary," approximately 72 km from the coast.

Eubothrium (? *crassum* Bloch, 1779)

Only three specimens of *Eubothrium* were collected, all from a single locality, at "Campsite Lake." Three out of four hosts examined from this lake harbored one *Eubothrium* each. Positive identification of this parasite to species level proved impossible due to the poor quality of the preserved fish from this locality. Hicks and Threlfall (1973) reported *E. crassum* in *S. alpinus* from Labrador.

Proteocephalus sp.

This cestode was collected from hosts at one lake and three stream localities. Species of *Proteocephalus* are known from *S. alpinus* in Labrador (Hicks and Threlfall 1973) and Quebec (Hanek and Molnar 1974).

Nematoda

Cystidicola stigmatura Skinker, 1931

Large numbers of *C. stigmatura* were present in the swim bladder of hosts from Joe Creek and the Shaviovik River. Among juvenile char that had not yet been to sea, intensity of infection increased with fish weight. In contrast, six large migrant fish from Joe Creek were free of *C. stigmatura*.

Bulbodacnitis alpinus Mudry and McCart, 1974

The description of *B. alpinus* was accompanied by distribution records obtained as part of the present study (Mudry and McCart 1974). Among nonmigrant fish, infection intensity tended to increase with fish weight. The six large migrant fish from Joe Creek harbored only four immature *B. alpinus*.

Acanthocephala

Metechinorhynchus salmonis Müller, 1784

All seven *S. alpinus* examined from Porcupine Lake harbored large numbers of *M. salmonis*. Van Cleave (1920) reported *M. salmonis* (as *Echinorhymcus coregoni*) from *S. alpinus* near Bernard Harbour, Northwest Territories.

Copepoda

Salmincola edwardsii Olsson, 1869

Salmincola edwardsii was found in small numbers in char from five of the seven streams sampled but was absent in char from the four lakes. Kabata (1969) considers *S. alpinus* to be a common host of *S. edwardsii*. The presence of *S. edwardsii* was usually associated with shortened gill filaments and excess amounts of mucus on the gills.

Salmincola carpionis Krøyer, 1837

Salmincola carpionis was found in only two localities, both streams. This parasite has been reported from *S. alpinus* from the eastern arctic (Kabata 1969) and Labrador (Hicks and Threlfall 1973).

Acknowledgments — We thank Mr H. Bain and Dr P. Craig of Aquatic Environments Limited for assistance in field collections; Dr H. P. Arai provided laboratory space for D.R.M.; Dr A. O. Dechtiar confirmed identification of *T. alaskensis*. We also thank Dr L. Margolis for critically reading the manuscript and providing helpful comments. Collection permits were provided by the Department of the Environment and the State of Alaska Department of Fish and Game. This study was supported by a National Research Council of Canada Grant.

BYCHOWSKY, B. E. 1957. Monogenetic trematodes, their systematics and phylogeny. 1961. Inst. Biol. Sci. Publ. 627 p. (Transl. from Russian)

BYKHOVSKAYA-PAVLOVSKAYA, I. E. 1962. Key to parasites of freshwater fish of the USSR. 1964. Israel Progr. Sci. Trans., Jerusalem. (Transl. from Russian)

HANEK, G., AND K. MOLNAR. 1974. Parasites of freshwater and anadromous fishes from Matamek River system, Quebec. J. Fish. Res. Board Can. 31: 1135–1139.

HICKS, F. J., AND W. THRELFALL. 1973. Metazoan parasites of salmonids and coregonids from coastal Labrador. J. Fish. Biol. 5: 399–415.

KABATA, Z. 1969. Revision of the genus *Salmincola* Wilson, 1915 (Copepoda: Lernaeopodidae). J. Fish. Res. Board Can. 26: 2987–3041.

MCCART, P., AND H. BAIN. 1974. An isolated population of Arctic char (*Salvelinus alpinus*) inhabiting a warm mineral spring above a waterfall at Cache Creek, Northwest Territories. J. Fish. Res. Board Can. 31: 1408–1414.

MCCART, P., AND P. CRAIG. 1971. Meristic differences between anadromous and freshwater-resident Arctic char (*Salvelinus alpinus*) in the Sagavanirktok River drainage, Alaska. J. Fish. Res. Board Can. 28: 115–118.

MCPHAIL, J. D. 1961. A systematic study of the *Salvelinus alpinus* complex in North America. J. Fish. Res. Board Can. 18: 793–816.

MUDRY, D. R., AND P. MCCART. 1974. *Bulbodacnitis alpinus* sp. nov. (Nematoda: Cucullanidae) from Arctic char, *Salvelinus alpinus* L., with notes on other species of *Bulbodacnitis*. Can. J. Zool. 52: 441–446.

SANDEMAN, I. M., AND M. D. B. BURT. 1972. Biology of *Bothrimonus* (=*Diplocotyle*) (Pseudophyllidae: Cestoda): ecology, life cycle, and evolution; a review and synthesis. J. Fish. Res. Board Can. 29: 1381–1395.

SCOTT, W. B., AND E. J. CROSSMAN. 1973. Freshwater fishes of Canada. Bull. Fish. Res. Board Can. 184: 966p.

VAN CLEAVE, H. J. 1920. Acanthocephala of the Canadian Arctic expedition, 1913–1918. Rep. Can. Arct. Exped. 1913–1918, 9, Part E: 1–11.

WARDLE, R. A. 1932. The Cestoda of Canadian fishes. II. The Hudson Bay drainage system. Contrib. Can. Biol. Fish., N.S. 7: 377–403.

Relation Between Yield and Fishing Mortality for Ricker's Yield Equation

A. L. JENSEN

School of Natural Resources, University of Michigan, Ann Arbor, Mich. 48104, USA

JENSEN, A. L. 1976. Relation between yield and fishing mortality for Ricker's yield equation. J. Fish. Res. Board Can. 33: 275–277.

A method is presented that can be applied to examine the relation between yield and magnitude of fishing mortality for Ricker's dynamic pool yield equation. The magnitude of fishing mortality is measured by the norm of the vector of interval specific instantaneous fishing mortality coefficients. The method is applied to a bluegill sunfish (*Lepomis macrochirus*) population.

JENSEN, A. L. 1976. Relation between yield and fishing mortality for Ricker's yield equation. J. Fish. Res. Board Can. 33: 275–277.

L'auteur décrit une méthode pouvant être appliquée à l'examen de la relation entre le rendement et l'importance de la mortalité due à la pêche pour l'équation de rendement de pools dynamiques de Ricker. Le degré de mortalité due à la pêche est mesuré par la norme du vecteur des coefficients spécifiques par intervalles de mortalité instantanée due à la pêche. L'auteur applique la méthode à une population de crapets arlequins (*Lepomis macrochirus*).

Received May 26, 1975
Accepted October 14, 1975

Reçu le 26 mai 1975
Accepté le 14 octobre 1975

IN this note a method is illustrated for study of the relation between yield and the intensity of fishing mortality for Ricker's dynamic pool model for yield from a fishery. Development and application of dynamic pool models for assessment of fish populations are discussed by Ricker (1975).

The simplest of the dynamic pool models is Ricker's (1945) model. Ricker's model has been applied to several fisheries. For example, Patriarche (1974) and Eschenroder and Haas (1974) applied Ricker's model to study the lake whitefish (*Coregonus clupeaformis*) in the Great Lakes, Sakawaga and Pycha (1971) applied the model to study the lake trout (*Salvelinus namaycush*) of Lake Superior, and Ketchen and Forrester (1966) applied Ricker's model to the petrale sole (*Eopsetta jordani*). Paulik and Bayliff (1967) developed a general computer program for Ricker's model.

Ricker's model is easy to apply. A drawback is that if the lifespan is divided into intervals it is difficult to examine yield from the recruited population as a function of fishing mortality.

Printed in Canada (J3847)
Imprimé au Canada (J3847)

There is a different fishing mortality coefficient for each interval. In this study it is shown that the relation between yield and the magnitude of the vector of fishing mortality can be applied to examine the relation between yield and fishing mortality.

Ricker's yield equation — Ricker (1945) divided the exploited lifespan of a fish into T intervals and applied the equation

$$Y_E = \sum_{i=1}^{T} F_i \bar{B}_i = \sum_{i=1}^{T} \frac{F_i B_i (e^{(g_i - Z_i)} - 1)}{g_i - Z_i} \quad (1)$$

to calculate the annual equilibrium yield. In equation (1) the terms are defined as:

Y_E = equilibrium annual yield in weight,
F_i = instantaneous fishing mortality coefficient during interval *i*,
B_i = biomass at beginning of interval *i*,
$\bar{B}_i$ = mean biomass during interval i,
g_i = instantaneous growth rate constant during interval *i*,
Z_i = instantaneous total mortality coefficient during interval *i*.

Ricker (1945) applied equation (1) to a bluegill sunfish (*Lepomis macrochirus*) population for study of the relation between size of fish when caught and yield.

The intervals in equation (1) can be years but this is not always desirable. The intervals should be constructed so that growth and fishing and natural mortality are relatively constant during the intervals. Ricker (1958) applied the model to the bluegill sunfish population using an interval of ¼ yr because large variations in growth and fishing mortality occurred during a year.

In vector terminology Ricker's yield equation can be expressed as the inner product of a vector of instantaneous fishing mortality rates and a vector of average biomass levels

$$Y_E = \sum_{i=1}^{T} F_i \bar{B}_i = (\bar{B}_1, \bar{B}_2, \ldots, \bar{B}_T) \begin{pmatrix} F_1 \\ F_2 \\ \vdots \\ F_T \end{pmatrix} \quad (2)$$

In analyses where all age-groups are combined, effort and mortality are related by the equation $F = qE$, in which q is a catchability constant, E is fishing effort, and F is the instantaneous fishing mortality coefficient. For Ricker's model a similar relation holds, i.e.

$$\vec{F} = \begin{pmatrix} F_1 \\ F_2 \\ \vdots \\ F_T \end{pmatrix} = E \begin{pmatrix} q_1 \\ q_2 \\ \vdots \\ q_T \end{pmatrix} = E\vec{q} \quad (3)$$

where the fishing effort E is a scalar quantity. Assuming that the catchability constants remain constant, an increase in effort results in the same increase in the instantaneous fishing mortality of each interval. The magnitude of the fishing mortality vector is measured by the vector norm which is represented as $\|\vec{F}\|$, and which is defined as

$$\|\vec{F}\| = \sqrt{F_1^2 + F_2^2 + \ldots + F_T^2} \quad (4)$$

From equation (3) it can be shown that

$$\|\vec{F}\| = E \, \|\vec{q}\| \quad (5)$$

Both the vector norm $\|\vec{F}\|$ and the vector norm $\|\vec{q}\|$ in equation (5) are scalers (i.e. numbers) and equation (5) states that the vector norm of the instantaneous fishing mortality rates is proportional to effort. The vector norm $\|\vec{F}\|$measures the magnitude of the fishing mortality. A change in fishing effort produces a change in $\|\vec{F}\|$ and a certain percentage change in $\|\vec{F}\|$ is accompanied by the same percentage change occurring in the instantaneous fishing mortality coefficients of each interval. To examine the relation between yield and fishing mortality the relation between yield and $\|\vec{F}\|$ can be examined.

Application to a bluegill sunfish population — Ricker (1975) has published age specific data for the bluegill sunfish sport fishery of Muskellunge Lake, Indiana. Table 1 lists the observed age structure, age specific weights, age specific instantaneous growth rates, age specific total instantaneous mortality rates, age specific natural mortality rates, and the yield calculated using equation (1). For simplicity the intervals in Table 1 are years rather than ¼ yr as in Ricker (1975).

To determine yield as a function of the rate of

TABLE 1. Age specific data for bluegill sunfish (*Lepomis macrochirus*) population of Muskellunge Lake, Indiana (modified from Ricker 1958). (Equilibrium yield [kilograms] per 1000 recruits = 28.89; $\|\vec{F}\| = 0.88$.)

Age	N	Wt	*g*	Z	F	Y
2	76923	13				
			1.67	0.77	0.62	1072
3	35333	69				
			0.46	1.09	0.36	672
4	11809	110				
			0.21	1.09	0.42	365
5	3971	137				
			0.14	2.22	0.30	91
6	430	158				

TABLE 2. Summary of bluegill population at two different levels of exploitation.

Age	N	B	F
	$\|\|\vec{F}\|\| = 0.353$		
2	76923	1000	
			0.248
3	51666	3564	
			0.144
4	21559	2371	
			0.168
5	9325	1277	
			0.120
6	1212	191	
	$\|\|\vec{F}\|\| = 1.413$		
2	76923	1000	
			0.992
3	24552	1694	
			0.576
4	6651	732	
			0.672
5	1738	238	
			0.480
6	158	25	

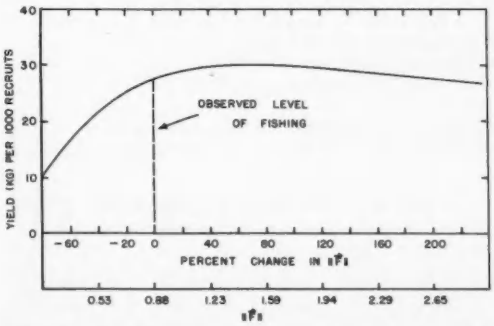

FIG. 1. Relation between annual equilibrium yield from a bluegill sunfish (*Lepomis macrochirus*) population and magnitude of fishing mortality as measured by the vector norm $\|\vec{F}\|$.

fishing mortality the norm of the vector of instantaneous fishing mortality coefficients, $\|\vec{F}\|$, was varied by increments of 10% from 80% below the observed value of $\|\vec{F}\|$ to far above the observed value of $\|\vec{F}\|$. At the observed rate of fishing the vector norm $\|\vec{F}\|$ was 0.883. Table 2 shows the changes in fishing mortality, age structure, and age specific biomass that occur with increasing fishing effort. At higher rates of fishing the number of older fish in the population decreases considerably.

The relation between yield per 1000 recruits and $\|\vec{F}\|$ is shown in Fig. 1. As the fishing effort increases the yield increases to a maximum and then slowly begins to decrease. The decrease in yield results from a decrease in the number of older and larger individuals. When all individuals are captured at recruitment the yield will equal the recruitment biomass of about 13 kg/1000 as compared to the maximum yield of about 30 kg/1000. Figure 1 shows that the population is underutilized, but that an increase in effort will not result in much increase in yield. Figure 1 is effective for summarizing the effect of fishing on the yield from a population for Ricker's model.

Ricker (1958, 1975) states that the equation

$$Y_E = \sum_{i=1}^{T} F_i \bar{B}_i = \sum_{i=1}^{T} \frac{F_i B_i (1 + e^{(g_i - Z_i)})}{2} \quad (6)$$

can also be applied to calculate yield. In equation (6) the average biomass is calculated as the arithmetic mean of the final and initial biomass levels. Equation (6) does not give the same results as equation (1). There is little difference between the results until $|g_i - Z_i|$ exceeds one; the differences then become increasingly large as values for $|g_i - Z_i|$ increase. Equation (1) is the correct form of Ricker's equation and equation (6) should not be used for simulation studies.

Acknowledgments — This study was supported by the University of Michigan Sea Grant Program.

BEVERTON, R. J. H., AND S. J. HOLT. 1957. On the dynamics of exploited fish populations. Fish. Invest. Minist. Agric. Fish. Food (G.B.) Ser. II Salmon Freshwater Fish. 20: 1–533.

ESCHENRODER, R. L., AND R. C. HAAS. 1974. Status of selected stocks of Lake Huron and recommendations for commercial harvest. Mich. Dep. Nat. Resour. Fish. Div. Tech. Rep. 73-32: 54 p.

KETCHEN, K. S., AND C. R. FORRESTER. 1966. Population dynamics of the petrale sole, *Eopsetta jordani*, in waters off western Canada. Bull. Fish. Res. Board Can. 153: 195 p.

PAULIK, G. J., AND W. H. BAYLIFF. 1967. A generalized computer program for the Ricker model of equilibrium yield per recruitment. J. Fish. Res. Board Can. 24: 249–259.

PATRIARCHE, M. H. 1974. Biomass of whitefish in northern Lake Michigan, 1971 and 1972. Mich. Dep. Nat. Resour. Fish. Rep. 1813: 15–20.

RICKER, W. E. 1945. A method of estimating minimum size limits for obtaining maximum yield. Copeia 2: 84–94.

1958. Handbook of computations for biological statistics of fish populations. Bull. Fish. Res. Board Can. 119: 300 p.

1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191: 382 p.

SAKAGAWA, G. T., AND R. L. PYCHA. 1971. Population biology of lake trout (*Salvelinus namaycush*) of Lake Superior before 1950. J. Fish. Res. Board Can. 28: 65–71.

Homing Behavior and Population Stratification in Central Puget Sound English Sole (*Parophrys vetulus*)

DWANE E. DAY

Washington State Department of Fisheries, Fisheries Center, University of Washington, Seattle, Wash. 98195, USA

DAY, D. E. 1976. Homing behavior and population stratification in central Puget Sound English sole (*Parophrys vetulus*). J. Fish. Res. Board Can. 33: 278–282.

Tag recovery data for a central Puget Sound English sole (*Parophrys vetulus*) tagging study in which fish captured at some locations were tagged and released at others suggested the homing of some fish back to their locations of capture. The occurrence of significant homing was verified through an analysis of tag recovery rates at locations of initial capture and locations of release during successive time intervals. The analysis also revealed that fish not displaced during tagging remained essentially at their locations of original capture. These observations evidenced ridged geographic stratification of the population represented by the tagged fish.

Both tag recovery data and catch-per-unit-effort data suggested the migration of some English sole out of the area and/or depths of fishing during fall–winter months.

DAY, D. E. 1976. Homing behavior and population stratification in central Puget Sound English sole (*Parophrys vetulus*). J. Fish. Res. Board Can. 33: 278–282.

Les recaptures de soles anglaises (*Parophrys vetulus*) du Puget Sound marquées lors d'une étude dans laquelle des poissons capturés à un endroit ont été marqués et remis à l'eau à un autre endroit donnent à croire qu'il y a «homing» de certains poissons vers l'endroit de capture. L'analyse des taux de recapture des marques aux endroits de capture initiale et aux endroits de remise à l'eau à intervalles de temps successifs nous ont permis de nous assurer qu'il y avait réellement homing. Cette analyse montre également que les poissons non déplacés après marquage demeurent essentiellement aux endroits de capture originelle. Ces observations démontrent l'existence d'une stratification géographique ridée de la population représentée par les poissons marqués.

Les recaptures de marques et les prises par unité d'effort suggèrent toutes deux qu'il y a mouvement de quelques soles hors des lieux et/ou des profondeurs de pêche pendant les mois d'automne et d'hiver.

Received May 15, 1975
Accepted October 21, 1975

Reçu le 15 mai 1975
Accepté le 21 octobre 1975

A preliminary examination of tag recovery for a 1964 English sole (*Parophrys vetulus*) tagging study in central Puget Sound revealed a tendency of fish captured at one site and released at another to return to their respective sites of capture. An annual migration of some English sole from the area of tagging northward during the winter was also suggested.

The discreteness of local populations of English sole in the "inside waters" of Washington state was first documented by Smith (1936) who demonstrated the populations in six different areas (Sequim Bay, Discovery Bay, Gulf of Georgia, Bellingham Bay, Penn Cove, and Hale Passage) to be discrete on the basis of meristics.

The discreteness of populations in other areas has subsequently been indicated by meristic, morphometric, and parasite distribution studies by Holland (1969), parasite distribution studies by Williams (1950), and by a number of tagging studies (Pruter and Van Cleve 1954; Van Cleve and Pruter 1956; Menasveta 1958; El-Sayed 1960; Van Cleve and El-Sayed 1969).

The homing of the displaced fish evident in the recoveries for the 1964 tagging study suggested that the division of Puget Sound's English sole population into discrete local populations did not end at the level of prominent bays and inlets.

To verify the homing behavior and also the apparent winter migration, the recovery data were analyzed in terms of the relative abundance of tagged fish at different sites and in different areas as indicated by the number of tag recoveries per unit of fishing effort.

Methods — Washington State Department of Fisheries personnel conducted tagging operations on board a commercial trawler during the period Sep-

Printed in Canada (J3830)
Imprimé au Canada (J3830)

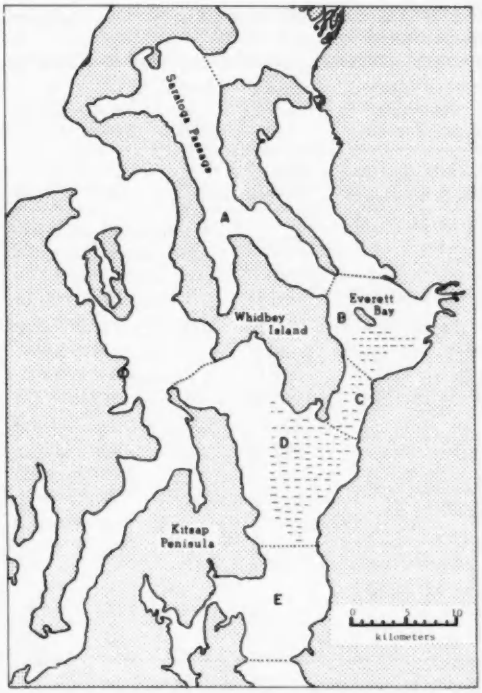

FIG. 1. Regional subdivisions of central Puget Sound. The general area of tagging operations is indicated by dashed lines.

tember 9 through 11, 1964 to obtain information on the migratory behavior and growth rate of central Puget Sound English sole. Some of the English sole catch of each drag was held in a deck tank for tagging. The remainder became part of the commercial catch. Fish in the tank were tagged, measured, and released during the subsequent drag or the run back to port. Thus, the location of fish release differed to varying degrees from the location of initial fish capture.

A total of 1500 English sole were tagged. Through March 1968, 215 tags with reliable recovery location information were returned. All were from fish captured in central Puget Sound.

The number of recoveries for individual drags was small. The distribution of fishing effort in the recovery areas was too uneven to assume that the distribution of recoveries realistically reflected the distribution of tagged fish. The recovery data were therefore analyzed in terms of tag recovery per unit effort rates for pooled drags representing major fish displacement and pooled drags representing relatively negligible displacement.

Fishing effort and frequencies of tag recoveries for each drag were tabulated by eight successive 1-yr time intervals overlapping by 9 mo (to smooth seasonal effects) and by three recovery location categories: the site of capture (fishing ground of capture and immediately adjacent grounds), the site of release (fishing ground of release and immediately adjacent grounds), and "other sites" (central Puget Sound fishing grounds not represented in corresponding site of capture and site of release definitions).

The area of tag recovery was divided into five regions based primarily on its geographic configuration (Fig. 1). Drags having site of capture and site of release definitions (Table 1) with less than two grounds in common were categorized as representing fish displacement. All others were categorized as representing no fish displacement.

Seven drags were in Region D, and one each in Regions B and C. Because the number of recoveries for Region B and C drags was insufficient for meaningful separate analysis, the analysis was restricted to the recovery data of Region D drags.

The data for Region D drags representing fish displacement were pooled and recovery rates (recoveries per thousand hours fished) were calculated (Table 2). Corresponding calculations were made for pooled Region D drags representing no fish displacement. The ratios of the rate for the different recovery location categories to the sum of the rates for all recovery location categories were then derived for drags representing displacement and drags representing no displacement and plotted against time.

Two boats, the M/V *Lemes* and M/V *Pt. Defiance*, accounted for approximately 80% of the English sole catch from Central Puget Sound during the tag recovery period. To determine if the apparent homing was an artifact of errors in the fishing effort and/or tag recovery records of one of these boats, their recovery rate ratios for drags representing fish displacement were plotted separately.

Seasonal movements of central Puget Sound English sole were investigated using tag recovery and effort data of the M/V *Lemes* and M/V *Pt. Defiance* for most of Region D. Seven successive 6-mo periods were defined, representing fall–winter (October–March) and spring–summer (April–September) halves of the year. Recovery rates (number of recoveries per 100 h fished) for the tags of drags representing no fish displacement were calculated and plotted against time periods. Corresponding CPUE values for central Puget Sound English sole were similarly plotted.

To investigate the possibility of a northward seasonal movement of fish from south of Whidbey Island (Region D) into Possession Sound and Everett Bay (Regions C and B, respectively), "seasonal" tag recovery rates for Region D drags representing no fish displacement were calculated and plotted for combined Regions B and C.

Results and discussion — The divergence of the regression lines for the recovery rate ratios for pooled drags representing displaced fish illustrated the homing of those fish to their original sites of capture over a prolonged period (Fig. 2). The null hypothesis for the regression of the ratios

TABLE 1. Fish capture and release operations for September 1964 central Puget Sound English sole (*Parophrys vetulus*) tagging. Grounds shared by sites of release and capture are underlined.

Tagging date	Site of capture definition (*ground codes*)	Depth range (*m*)	Region of capture	Site of release definition (*ground codes*)	Depth range (*m*)	Region of release	No. released	No. recovered
Sept. 9, 1964	21, 24, 26, 46, 47, 51	97–220	D	2, 12, 16, 21, 26, 37, 46, 47, 48, 61	156–220	D	224	20
Sept. 9, 1964	2, 12, 16, 21, 26, 37, 46, 47, 48, 61	156–220	D	16, 17, 18, 25, 39, 41, 43	27–183	C	262	61
Sept. 9, 1964	16, 17, 18, 25, 39, 41, 43	27–183	C	1, 30, 35, 40	88–183	B	83	28
Sept. 9, 1964	1, 30, 35, 40, 41	88–183	B	21, 24, 26, 46, 47, 51	97–220	D	171	18
Sept. 9, 1964	21, 24, 26, 46, 47, 51	97–220	D	2, 12, 16, 21, 26, 37, 46, 47, 48, 61	156–220	D	69	7
Sept. 9, 1964	2, 12, 16, 21, 26 37, 46, 47, 48, 61	156–220	D	1, 17, 18, 25, 30, 35, 39, 40, 41, 43	27–183	C–B	142	19
Sept. 9, 1964	2, 12, 16, 21, 26 37, 46, 47, 48, 61	156–220	D	2, 12, 21, 38, 42 46, 46, 48, 61	156–220	D	191	18
Sept. 9, 1964	2, 12, 21, 38, 42 46, 47, 48, 61	156–220	D	2, 12, 16, 21, 26 37, 46, 47, 48, 61	156–220	D	193	27
Sept. 9, 1964	2, 12, 16, 21, 26 37, 46, 47, 48, 61	156–220	D	1, 17, 18, 25, 30 35, 39, 40, 41, 43	27–183	C–B	164	25
Total Fish							1500	223

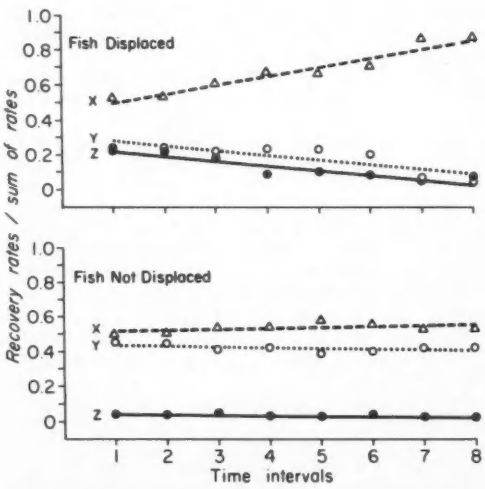

FIG. 2. Ratios of tag recovery rates for pooled sites of capture X, pooled sites of release Y, and pooled "other sites" Z to each other for consecutive 9-mo overlapping 1-yr time intervals.

for the displaced fish at their site of capture was rejected at the 99% confidence level ($t = 8.85$, 6 df). The maintenance of the recovery rate ratios at the constant levels illustrated in the plots of ratios representing fish not displaced demonstrated that these fish remained at their site of capture and site of release locations and did not disperse appreciably to other grounds.

The divergence of regression lines for the data of each of the two boats responsible for most of the recoveries demonstrated that the apparent homing was not a result of erroneous data for one of those boats (Fig. 3).

Although not included in the analysis, the recovery data of the single Region B drag evidenced homing behavior in the fish of that region. Of the 18 recoveries for that drag, only two were from the release site in Region D. The remainder were all from the site of original capture in Region B.

The analysis revealed a rigid geographic stratification of the central Puget Sound English sole population maintained by behavioral characteristics of the fish. The pronounced homing of the displaced fish suggests that resident Puget Sound English sole may be territorial and the population stratification extends down to the level of the individual territory. If this is the case, some of the local populations considered discrete on the basis of other tagging studies may actually be geographic extensions of the same larger stratified population.

The possibility of an annual migration out of Region D during fall–winter months was suggested by the apparent tendency for lower tag

TABLE 2. Derivation of tag recovery rates (recoveries per 1000 h fished) for different recovery location categories in successive time intervals for fish displaced from their sites of capture.

	Time intervals							
	1	2	3	4	5	6	7	8
	July/64–June/65	Oct./64–Sept./65	Jan./65–Sept./65	Apr./65–Mar./66	July/65–June/66	Oct./65–Sept./66	Jan./66–Dec./66	Apr./66–Mar./67
Pooled recoveries at:								
Sites of capture	25	23	14	14	11	15	18	18
Sites of release	20	16	6	6	4	4	1	1
"Other sites"	26	22	7	3	2	2	1	1
Pooled hours at:								
Sites of capture	1290.0	1359.3	1695.3	1696.8	2100.0	2251.5	3014.7	3054.3
Sites of release	2169.8	2174.3	2070.5	2123.1	2171.0	2083.8	2253.8	2538.9
"Other sites"	3148.7	3144.8	2774.2	2677.1	2602.8	2562.5	2317.6	2190.6
Recovery rate for pooled:								
Sites of capture	19.38	16.92	8.26	8.25	5.24	6.66	5.97	5.89
Sites of release	9.22	7.36	2.90	2.83	1.84	1.92	0.44	0.39
"Other sites"	8.26	7.00	2.52	1.12	0.77	0.78	0.43	0.46
Sum of recovery rates	36.86	31.28	13.68	12.20	7.85	9.36	6.84	6.74

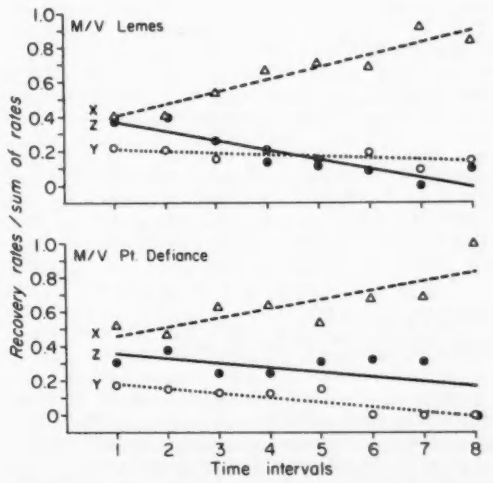

FIG. 3. Ratios of displaced fish tag recovery rates for pooled sites of capture X, pooled sites of release Y, and pooled "other sites" Z for consecutive 9-mo overlapping 1-yr time intervals.

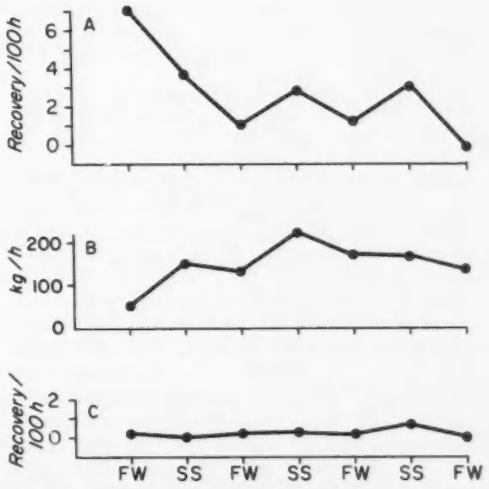

FIG. 4. "Seasonal" (fall–winter, spring–summer) distribution of A, Region D tag recovery rates for fish not displaced; B, Region D English sole (*Parophrys vetulus*) CPUE values; C, Combined Regions B and C tag recovery rates for Region D fish not displaced.

recovery rates and English sole CPUE values during that "season" (Fig. 4). The relatively high tag recovery rate for the first "season" does not conform, but the occurrence of a high tagging mortality during that period and/or a disruption of the migratory behavior of the tagged fish due to the effects of tagging could account for this. The consistently low recovery rates for Region D fish in combined Regions B and C indicated that the migration was not northward into these areas. If a migration did occur it had to be to areas and/or depths not intensively fished.

Acknowledgments — I thank J. Beam of the Washington Department of Fisheries for his considerable assistance in procuring and processing the fishing effort data essential to the analysis.

EL SAYED, S. Z. 1960. Population dynamics of English sole (*Parophrys vetulus* Girard) in Puget Sound, Washington, with special reference to the problems of sampling. Contr. Fish. Res. Inst., Seattle, Wash. 77: 40–41.

HOLLAND, G. A. 1969. Age, growth and mortality of races of English sole (*Parophrys vetulus*) in Puget Sound, Washington. Bull. Pac. Mar. Fish. Comm. 7: 35–50.

MENASVETA, D. 1958. Migration and fishing mortality of English sole (*Parophrys vetulus*) in Saratoga Passage, and adjacent waters. M.Sc. Thesis. Univ. Washington, Seattle, Wash. 84 p.

PRUTER, A. T., AND R. VAN CLEVE. 1954. A preliminary study of the population of English sole, *Parophrys vetulus*, in Holmes Harbor, Washington. Wash. Dep. Fish., Fish. Res. Pap. 1: 3–18.

SMITH, R. T. 1936. Report on the Puget Sound otter trawl investigations. Wash. Dep. Fish. Biol. Rep. 36: 1–66.

VAN CLEVE, R., AND A. T. PRUTER. 1956. Problems of sampling a Puget Sound population of English sole, *Parophrys vetulus*. Rapp. P.-V. Reun., Cons. Int. Explor. Mer 140: 87–93.

VAN CLEVE, R., AND S. Z. EL SAYED. 1969. Age, growth and productivity of an English sole (*Parophrys vetulus*) population in Puget Sound, Washington. Bull. Pac. Mar. Fish. Comm. 7: 51–71.

WILLIAMS, R. W. 1950. The bottom fishery and otter trawling. Wash. Dep. Fish. Ann. Rep. 1949: 88–90.

Role of Rearing Experience in Gravel Substrate Selection by Juvenile Rainbow Trout, *Salmo gairdneri*

HUGH R. MACCRIMMON

Department of Zoology, College of Biological Science, University of Guelph, Guelph, Ont. N1G 2W1

AND CHRISTOPHER M. HAWKINS

Marine Science Centre, McGill University, Montreal, Que.

MACCRIMMON, H. R., AND C. M. HAWKINS. 1976. Role of rearing experience in gravel substrate selection by juvenile rainbow trout, *Salmo gairdneri*. J. Fish. Res. Board Can. 33: 282–284.

Laboratory studies on hatchery-reared wild juvenile rainbow trout (*Salmo gairdneri*) in an experimental raceway show no significant selection ($P < 0.05$) of test gravel substrates under either nonflowing or flowing (0.03 m/s) conditions regardless of rearing experience. There is no statistical evidence that hatchery conditioning of rainbow trout for gravel substrate selection is likely to be a feasible undertaking.

MACCRIMMON, H. R., AND C. M. HAWKINS. 1976. Role of rearing experience in gravel substrate selection by juvenile rainbow trout, *Salmo gairdneri*. J. Fish. Res. Board Can. 33: 282–284.

Des études de laboratoire effectuées dans un dalot expérimental sur de jeunes truites arc-en-ciel (*Salmo gairdneri*) n'indiquent pas de sélection significative ($P < 0.05$) de substrats de gravier ni en eau morte ni en eau courante (0.03 m/s), quelle que soit l'expérience acquise au cours de l'élevage. On ne peut prouver statistiquement que le conditionnement de la truite arc-en-ciel vers le choix d'un substrat de gravier soit chose faisable.

Received June 9, 1975
Accepted October 17, 1975

Reçu le 9 juin 1975
Accepté le 17 octobre 1975

SEVERAL studies have related gravel substrate to the survival and distribution of young stream salmonids (Allen and Clarke 1943; MacCrimmon 1954; Edmundson et al. 1968; Alexander and MacCrimmon 1974). However, there has been no quantitative laboratory study to determine the direct relation, if any, between gravel size and substrate selection by juvenile trout. If specific gravel substrate selection occurs, then this phenomenon could be used to advantage in the design of hatchery-rearing facilities, and in improving natural stream habitats by providing substrates of appropriate gravel size. Further, the possibility of preconditioning hatch-

Printed in Canada (J3868)
Imprimé au Canada (J3868)

ery-reared salmonids to utilize natural or artificially created gravel substrates is a matter of considerable interest to fisheries managers.

The objective of the present laboratory study, therefore, was to determine if juvenile rainbow trout, *Salmo gairdneri*, exhibit a preference for gravel size, and if previous exposure to a specific gravel size has a conditioning effect on subsequent substrate selection.

Materials and methods — Rainbow trout eggs of the Normandale stock, divided into four groups, were incubated in three sizes of gravel substrate and in a hatchery basket over a smooth bottom. After hatching, each lot was reared in its respective natal trough for a minimum of 50 wk at 12 C before testing. Wild rainbow trout, obtained from a Georgian Bay tributary by electrofishing, were held in smooth-bottomed fiberglass troughs for 1 mo prior to testing. A photoperiod of 12 h each of light and dark was maintained in both rearing and testing facilities.

Tests on gravel substrate selection were done in an elliptical plexiglass raceway 45.0 cm wide with a water depth of 20.3 cm (Hawkins 1974). Two testing chambers, each 129.3 cm in length and confined by screens, were located on each side of the raceway. Each chamber contained three interchangeable plates (1858 cm^2) with a specific substrate achieved by adhering gravel of 1.6 cm (small), 3.4 cm (medium), and 6.2 cm (large) diam to the plate. Tests were run under nonflowing and flowing conditions. A continuous current of 0.03 m/s, when required, was provided by a paddle wheel positioned at one end of the raceway. Water temperature was maintained at 10 C by a water exchange system which set up no appreciable current in the test compartments. Dissolved oxygen levels were maintained at 10 ppm by the air injection of inflowing water. A water surface illumination of 3205 lx was provided by fluorescent lights positioned above the test compartments.

Data were recorded using two 8-mm Sankyo movie cameras located above the test compartments to record the precise position of test fish. The cameras and tungsten bulbs were activated automatically at 10-min intervals, giving 144 exposures within each 24-h test period. Exposures were for 0.5 s with a floodlight flash of 1.4 s (surface illumination of 7148 lx) which had no apparent effect on behavior. Pictures taken by single frame photography on Kodak Ectochrome 160 film were time coded for subsequent viewing through a "Dual Eight" film editor.

Analysis of variance was carried out on response values of all fish exposed to the three test substrates under nonflowing and flowing conditions. On indication of significance at the 0.05 level, Scheffe's Test was used to determine specific substrate selection by individual fish groups. Possible effects of the experimental facility on fish positioning within each test compartment was overcome by positioning the substrates orthogonally (Snedecor and Cochran 1967). Sample size for each experiment was six fish per group, each fish being tested singly and used only once, i.e. 144 observations per fish, 864 observations per group.

Results — An analysis of the response of test fish to the three sizes of gravel substrate (Table 1) reveals no significant difference among test groups of hatchery-reared fish with different rearing experiences in the selection of these substrates under either flowing or nonflowing conditions. Neither does the response of wild fish to gravel substrate show a specific selection; nor does their response differ significantly from that of hatchery-reared fish with but one exception, namely, between wild fish and those hatchery-reared fish lacking previous gravel exposure, and only then under flowing conditions.

The influence of rearing experience on gravel substrate selection within any test group of wild or hatchery-reared fish under either a flowing or nonflowing water condition, is not significant ($P < 0.05$). However, an inspection of the data indicates that there were apparent differences, although statistically unverified, in substrate selection between groups of fish tested under flowing and nonflowing conditions.

Discussion — The failure of test juvenile rainbow trout to respond significantly to a choice of gravel substrates is surprising to the authors in view of the findings of previous laboratory experiments which identified predictable selective responses to trout exposed to a choice of bottom coloration (Kwain and MacCrimmon 1967; Ritter and MacCrimmon 1973a). The difference in results suggests that either the visual acuity whereby the fish distinguish black and white backgrounds (Kwain and MacCrimmon 1969) does not extend to an identification of gravel size, or that fish held in the experimental raceway were not exposed to stress–fright stimuli which were found to increase the level of bottom selection in previous experiments.

While there is not statistical proof ($P > 0.05$) that the test fish had the ability to discern available gravel sizes, the data do provide evidence of increased substrate selection by the trout under flowing vs. nonflowing conditions. Hence, flow is probably an important factor in explaining observed affinities of juvenile salmonids to gravel riffles under natural stream conditions (Alexander and MacCrimmon 1974; Edmundson et al. 1968; Jenkins 1969; MacCrimmon 1954). Failure of the test fish to exhibit a significant gravel selection in the experimental raceway suggests that commonly observed occurrences of juvenile trout

TABLE 1. Mean number of observations recorded for 24-h periods over each gravel substrate texture by groups of rainbow trout (*Salmo gairdneri*) examined under flowing and nonflowing water conditions. (Values in parentheses indicate 0.05 confidence limits.)

	Relative selection of substrate texture					
	Nonflowing system			Flowing system		
	Substrate texture			Substrate texture		
Groups of fish	Small (±17.62)	Medium (±22.56)	Large (±22.00)	Small (±17.62)	Medium (±22.56)	Large (±22.00)
Reared in small gravel	51.19	24.68	23.39	33.03	36.32	33.85
Reared in medium gravel	22.91	41.54	31.07	37.62	35.59	27.87
Reared in large gravel	30.92	36.82	30.11	36.58	30.30	34.78
Reared without gravel	25.41	27.66	47.37	47.98	25.83	27.61
Wild (held without gravel)	35.04	40.38	20.68	13.04	22.41	59.00
Composite (average of all groups tested)	27.68	34.22	30.52	33.65	30.09	36.62

over gravel bottoms in natural streams may be the result of a combination of environmental inputs (MacCrimmon 1954), rather than a simple selection of gravel substrate.

Despite earlier findings (Ritter and MacCrimmon 1973b) that juvenile rainbow trout may be conditioned for wariness, as measured by their subsequent selection of black and white substrates, the present study gives no statistical evidence that hatchery conditioning of trout for gravel substrate preference is likely to be a feasible undertaking.

ALEXANDER, D., AND H. R. MACCRIMMON. 1974. Production and movement of juvenile rainbow trout (*Salmo gairdneri*) in a headwater of Bothwell's Creek, Georgian Bay. J. Fish. Res. Board Can. 31: 117–121.

ALLEN, W. R., AND M. E. CLARK. 1943. Bottom preferences of fishes of north eastern Kentucky streams. Trans. Ky. Acad. Sci. 11: 26–30.

EDMUNDSON, E., F. E. EVEREST, AND D. W. CHAPMAN. 1968. Permanence of station in juvenile chinook salmon and steelhead trout. J. Fish. Res. Board Can. 25: 1453–1464.

HAWKINS, C. 1974. Role of yearling experiences in gravel substrate selection by juvenile rainbow trout, *Salmo gairdneri* Richardson. M.Sc. Thesis. Univ. Guelph, Guelph, Ont. 48 p.

JENKINS, T. M. JR. 1969. Social structure, position choice and microdistribution of two trout species (*Salmo trutta* and *Salmo gairdneri*) resident in mountain streams. Anim. Behav., Monogr. 2: 57–123.

KWAIN, W., AND H. R. MACCRIMMON. 1967. The behaviour and bottom colour selection of the rainbow trout, *Salmo gairdneri* Richardson, exposed to different light intensities. Anim. Behav. 15: 75–78.

1969a. Age and vision as factors in bottom colour selection by rainbow trout, *Salmo gairdneri*. J. Fish. Res. Board Can. 26: 687–693.

MACCRIMMON, H. R. 1954. Stream studies on planted Atlantic salmon. J. Fish. Res. Board Can. 11: 362–403.

RITTER, J. A., AND H. R. MACCRIMMON. 1973a. Influence of environmental experience on the response of yearling rainbow trout (*Salmo gairdneri*) to a black and white substrate. J. Fish. Res. Board Can. 30: 1740–1742.

1973b. Effects of illumination on behaviour of wild brown trout (*Salmo trutta*) and rainbow trout (*Salmo gairdneri*) exposed to black and white backgrounds. J. Fish. Res. Board Can. 30: 1875–1880.

SNEDECOR, G. W., AND W. G. COCHRAN. 1967. Statistical methods. 6th ed. Iowa State University Press, Ames, Iowa. 267–268.

Changes in Some Hematological Characteristics of Coho Salmon (*Oncorhynchus kisutch*) in Response to Acute Exposure to Dehydroabietic Acid (DHAA) at Different Exercise Levels

GEORGE K. IWAMA

Department of Zoology, The University of British Columbia, Vancouver, B.C. V6T 1W5

G. L. GREER

Pacific Environment Institute, West Vancouver, B.C. V7V 1N6

AND P. A. LARKIN

Institute of Animal Resource Ecology, The University of British Columbia, Vancouver, B.C. V6T 1W5

IWAMA, G. K., G. L. GREER, AND P. A. LARKIN. 1976. Changes in some hematological characteristics of coho salmon (*Oncorhynchus kisutch*) in response to acute exposure to dehydroabietic acid (DHAA) at different exercise levels. J. Fish. Res. Board Can. 33: 285–289.

To determine if changes in some hematological parameters accompanied acute exposure of juvenile coho salmon (*Oncorhynchus kisutch*) to dehydroabietic acid (DHAA) at three different exercise levels, clotting times, hematocrits, erythrocyte sedimentation rates, red blood cell counts, and white blood cell counts were monitored over 6-, 12-, 24-, and 48-h exposure periods to 0.75 mg/liter DHAA.

White cell counts decreased significantly after 24 h exposure and there was a significant increase in clotting times after 48 h exposure to DHAA. In both cases, differences between experimentals and controls were significant only at low and intermediate exercise levels and not at a high exercise level. Hematocrits, erythrocyte sedimentation rates, and red blood cell counts were not significantly different between experimentals and controls for any of the exposure periods or exercise levels.

IWAMA, G. K., G. L. GREER, AND P. A. LARKIN. 1976. Changes in some hematological characteristics of coho salmon (*Oncorhynchus kisutch*) in response to acute exposure to dehydroabietic acid (DHAA) at different exercise levels. J. Fish. Res. Board Can. 33: 285–289.

En vue de déterminer si des changements dans les paramètres hématologiques accompagnaient une exposition aigue de jeunes saumons coho (*Oncorhynchus kisutch*) à l'acide déshydroabiétique (ADHA) à trois paliers différents d'exercice, nous avons mesuré les temps de coagulation, hématocrites, taux de sédimentation des érytrhocytes et comptes de globules rouges et de globules blancs (thrombocytes) du sang pendant des expositions de 6, 12, 24 et 48 h à 0.75 ppm d'ADHA.

Les globules blancs augmentent de façon significative après une exposition de 24 h, et il y a diminution significative des temps de coagulation après exposition de 48 h à l'ADHA. Dans les deux cas, les différences entre les poissons expérimentaux et les témoins ne sont significatives qu'au bas niveau et au niveau intermédiaire d'exercice et non au niveau élevé. Les hématocrites, les taux de sédimentation des érythrocytes et les comptes de globules rouges du sang n'accusent pas de différences significatives entre les poissons exposés et les témoins, quels que soient la période d'exposition ou le niveau d'exercice.

Received July 29, 1975
Accepted November 13, 1975

Reçu le 29 juillet 1975
Accepté le 13 novembre 1975

IN studies to develop short-term sublethal bioassays suitable for routine monitoring of kraft pulpmill effluents, several biochemical and hematological characteristics of juvenile coho salmon (*Oncorhynchus kisutch*) have been used as physiological indicators of stress resulting from exposure to this pollutant (McLeay 1973a; McLeay and Brown 1975). Because kraft effluents comprise mixtures highly variable in their sublethal (Davis 1973) and acutely toxic (Davis and Mason 1973) effects on fish, it is desirable

Printed in Canada (J3928)
Imprimé au Canada (J3928)

to attempt to evaluate sublethal effects of known effluent components in purified form.

Dehydroabietic acid (DHAA) is one of several naturally occurring resin acids extracted from softwood trees during the kraft process and is present mainly in unbleached white water, the major waste stream from the pulping section of a kraft mill (Rogers 1973; Rogers et al. 1975; Leach and Thakore 1973a). Its 96-h LC 50 (static bioassay) for juvenile freshwater coho is 1.4–1.8 mg/liter (Davis and Hoos 1975). The concentration of DHAA in mill effluents is highly variable and depends on species composition and storage history of wood furnish and whether the effluent undergoes biological treatment. In samples of unbleached white water from mills in British Columbia and Ontario, Leach and Thakore (1973b) found DHAA in concentrations ranging from 0.5 to 15.1 mg/liter.

This study was undertaken to determine if some hematological characteristics of juvenile coho salmon would reflect stress that might result from acute exposure to DHAA. Since natural environmental factors may impose nonlethal stress which could modify toxic or sublethal effects of a pollutant, the experiment was designed to test whether exercise level would influence the effect of DHAA on hematological characteristics.

Materials and methods — Juvenile coho salmon, of length 10.91 ± 0.97 cm and weight 14.07 ± 3.47 (mean ± SD) reared from eggs of wild stock returning to the Pacific Environment Institute, were held under natural photoperiod in a 1600-gal outdoor tank receiving Cypress Creek water, 2–5 C. Temperature adaptation of fish to the laboratory well-water supply (14.8–15.3 C; pH 6.8–6.9; O_2 8–8.5 mg/liter; hardness 54 mg/liter $CaCO_3$) used in the DHAA exposures was done in three steps. For each experiment, 75 fish were placed in a smaller tank containing creek water that was gradually substituted over 5–6 h with well water until the temperature was 10–10.5 C; the fish were transferred to a laboratory holding tank at 13 C for 18–20 h and 35 fish then placed in each of two 55-liter fiberglass annular tanks (39.5 cm diam, 19 cm annulus, 16 cm deep). In the annular tanks the fish were continuously exercised at different levels by controlling the output of recirculating pumps that maintained rotational movement of water in the tanks (Kruzynski 1972). Fish were not fed after removal from the outdoor tank. The experiments were done over the period late February to late April 1975.

After a 4-day period of acclimatization to the annular tanks and exercise levels, the fish were exposed under flow-through conditions to 0.75 mg/liter DHAA (94.6% purity) added to the tanks in the form of the sodium salt of the organic acid. DHAA was purified from a mixture of resin acids (Hercules Pine and Paper Department, Wilmington, Delaware) by the method of Halbrook and Lawrence (1966). The concentrated stock solutions of DHAA (2.25 g, dissolved in 100 ml 95% ethanol, 10 ml 5 N NaOH, 14.89 liters distilled water) were added to the tank diluent water (0.5 liters/min) inlet stream at the rate of 2.5 ml/min. The control tanks received the same quantities of ethanol and sodium hydroxide, in the same manner, but not DHAA. The pH of the water in the control and test tanks were not changed by addition of the control and DHAA stock solutions. At the start of an exposure period, 275 ml of control or DHAA stock solution was mixed in the appropriate tank to step the ambient concentration to the required value. Three levels of continuous exercise were investigated for both control and DHAA exposed fish: "high," 1.97 b.l. (body lengths)/s; "intermediate," 1.25 b.l./s; and "low," 0.5 b.l./s. The low exercise level was replicated once.

For each exercise level, eight fish from the experiment and eight from the control tanks were netted, one at a time, at 6, 12, 24, and 48 h after the start of the DHAA treatment. Each fish was then anesthetized (ca. 3 min) in 150 mg/liter tricane methane sulphonate (M.S. 222, Kent Laboratories, Vancouver, B.C.) neutralized with NaOH. The caudal peduncle was immediately dried with a tissue dampened with 95% ethanol, severed, and blood collected into a heparinized capillary tube (for ESR), an unheparinized capillary tube (clotting time), and a blood-diluting pipette (red and total white cell counts). Fork lengths and wet weights were measured after the blood had been collected. The sampling and hematological measurements for each group of experimental fish and their respective controls took about 4 h.

Clotting times were measured by the capillary tube method (Poston 1964) using scored unheparinized 25-μl microsampling pipettes. Erythrocyte sedimentation rates (ESR) were measured by the Micro-Wintrobe Method (Blaxhall and Daisley 1973) using 75 × 1.0–1.25 mm heparinized capillary tubes. Hematocrits were measured by the standard microhematocrit technique as described by Snieszko (1960) using the ESR tubes after the ESR readings were taken. Total white blood cell counts (which includes thrombocytes) and red blood cell counts were made using a standard red cell-diluting pipette (1:200 dilution), Rees-Ecker diluting solution (Klontz and Smith 1968), and hemocytometer. Red cell counts were multiplied by 10,000 and white cell counts by 500 to give the number of cells per mm^3 (Hesser 1960).

Means and standard deviations were calculated for each parameter for each of the sampling periods. Students *t*-test was used to test differences between experimental fish and their respective controls with $\alpha = .05$.

Results and discussion — During the 4-day period of acclimatization to the exercise levels, and before exposure to DHAA, the fish appeared to behave normally. Most of the fish held position in the water current in loosely collected groups.

TABLE 1. Mean clotting time ($\bar{x} \pm s$) in seconds for controls and for juvenile coho salmon (*Oncorhynchus kisutch*) continuously exposed to 0.75 mg/liter DHAA for various lengths of time at three different levels of exercise. Sample size 8, except where indicated by number in parentheses. Differences between experimentals and controls statistically significant for comparisons in boxed area ($\alpha = .05$).

Time (*h*)	Treatment	Level of exercise: Low, Replicate 1	Low, Replicate 2	Intermediate	High
6–10	Experimental	49.2± 1.6	65.4± 8.6	81.3±9.3	85.4± 4.5
	Control	75.3±12.8(7)	51.8± 3.9	66.4±7.4	96.1±10.3
12–16	Experimental	57.2± 2.2	96.3±11.2	86.0±6.3	98.2± 8.9
	Control	85.4±14.0	70.0± 9.3	71.7±7.9	100.1± 6.4
24–28	Experimental	63.4± 5.7	104.5±13.9	96.3±6.8	64.1± 2.9
	Control	69.4± 5.1	100.6± 8.1	86.2±8.3	74.0± 6.0
48–52	Experimental	139.6± 9.0(6)	126.0±14.5(7)	90.3±7.6	73.5± 5.6
	Control	99.8±10.8(7)	83.0± 7.0	60.2±7.7	63.2± 4.5(7)

On sudden presentation of a shadow or moving object over the annular tanks all fish quickly retreated beneath the cover provided. The fish were not forced to maintain position in the current and some individuals drifted slowly while maintaining positive rheotoxis, or favored positions near the inner wall of the annulus where the angular velocity of water was lower. Hence the rate of exercise performed by the fish, although continuous, was variable and on average probably less than indicated by the three water velocities used in the experiments.

By the 48th hour of exposure to 0.75 mg/liter DHAA, the behavior of the fish at the intermediate and low exercise levels changed. At the intermediate level fish in the experimental tank exhibited sluggish and disoriented behavior. In both replicates at the low exercise level swimming coordination seemed to be extremely poor and during sampling the fish lent themselves to capture without resistance. Mortalities during the course of the experiments occurred only at the low exercise level. Four and two fish were dead in replicates 1 and 2, respectively, by the 48th hour of exposure. There were neither mortalities nor unusual behavior in the high exercise and control groups of fish.

There were significant differences between control- and DHAA-exposed fish at the low and intermediate exercise levels for two of the five hematological characteristics measured. Mean clotting time had increased by 48 h of exposure; the differences between experimental and control fish being most marked at the low exercise level (Table 1). Total white blood cell counts decreased by the 24th hour of exposure (Table 2). Erythrocyte sedimentation rates, hematocrit values, and red cell counts for experimental fish did not differ significantly from their respective controls. Consistently for both experimentals and controls, erythrocyte sedimentation rates ranged from 0.5 to 1.5 mm/h hematocrits from 43 to 55%, and red blood cell counts from 1.1 to 1.6 million/mm^3.

A decrease in total white cell counts has also been reported for juvenile coho stressed by a 12-h exposure to one half the 96-h LC 50 of kraft mill effluent (McLeay 1973a). Using the technique of differential cell counting in that study, the decrease in total white cell count was determined to have been due mainly to reduction in the number of circulating small lymphocytes. This lymphopenic response is thought to result from a stress-mediated increase in secretion of corticosteroids by the interrenal tissue (McLeay 1973a). Both stress and corticosteroid administration have been shown to cause lymphopenia in salmonids (Weinreb 1958; McLeay 1970, 1973b, c). The decreased total white cell counts for coho exposed to DHAA for 24 h (Table 2) indicate that a state of stress was present at the low and intermediate exercise levels by that time. This stressed state also preceded by approximately 24 h behavioral signs of stress and, at the low exercise level, beginning mortalities.

The increased blood clotting times in coho after 48 h exposure to DHAA (Table 1) may have resulted from fewer circulating thrombocytes, a blood cell type thought to function in the clotting process (Gardner and Yevich 1969). A thrombocytopenic response also occurs in salmonids subjected to stress of corticosteroid administration (Weinreb 1958; McLeay 1970, 1973c). Thrombocytopenia would be reflected in

TABLE 2. Mean total white blood cell count ($\bar{x} \pm s$; no./mm^3 = x 10^4) for controls and for juvenile coho salmon continuously exposed to 0.75 mg/liter DHAA for various lengths of time at three different levels of exercise. Sample size 8, except where indicated by number in parentheses. Differences between experimentals and controls statistically significant for comparisons within boxed area. ($\alpha = .05$)

Time (*h*)	Treatment	Level of exercise: Low, Replicate 1	Low, Replicate 2	Intermediate	High
6–10	Experimental	5.15±0.49	5.89±1.26	3.72±0.25	5.30±1.06(7)
	Control	4.94±0.44	4.81±0.20	3.80±0.12	4.57±0.67
12–16	Experimental	4.74±0.45	3.27±0.40	2.61±0.22	2.92±0.47(7)
	Control	4.79±0.70	4.40±0.32(7)	3.22±0.23	3.35±0.43(7)
24–28	Experimental	2.69±0.29	2.93±0.45	1.96±0.13	2.54±0.45
	Control	5.17±0.45	4.06±0.21	4.37±0.40	3.71±0.60
48–52	Experimental	1.21±0.09(6)	1.19±0.18(7)	0.79±0.14	5.58±0.87(7)
	Control	6.44±0.95	4.51±0.36	4.26±0.46	5.86±0.70(7)

lower total white cell counts but could not be distinguished from lymphopenia by employing only hematocytometric counting as was done in the present study. Weinreb (1958) found that the lymphopenic response in rainbow trout (*Salmo gairdneri*) occurred 6 h after the onset of stress while the thrombocytopenic response followed about 40 h later. If delayed thrombocytopenia relative to lymphopenia is characteristic of all salmonids, a thrombocytopenic condition may have led to the increased clotting times by the 48th h of exposure to DHAA at the low and intermediate exercise levels. This same condition could have contributed to the further lowering of total white cell counts indicated in Table 2 for the 24th–48th hours of exposure.

The concentration of DHAA used in the present study is about 37% of the quantity found in effluent from a coastal kraft mill by Leach and Thakore (1973a). Although higher than the 96-h LC50 for juvenile sockeye (*O. nerka*) determined by flow-through bioassays (0.5 mg/liter; G. M. Kruzynski personal communication), 0.75 mg/liter was estimated to be near the flow-through 96-h LC50 for juvenile coho and a concentration that might be stressful within approximately 48 h. The changed behavior and mortalities noted at the low exercise level suggest 0.75 mg/liter DHAA is incipiently toxic to juvenile coho within about 48 h exposure under flow-through conditions. Higher levels of exercise appear to confer some measure of resistance to the toxic effect of DHAA.

The hematological results of the experiment suggest that increased clotting times and decreased total white blood cell counts can be used as indicators of stress experienced by juvenile coho during acute exposure to DHAA. Total white cell count is an earlier indicator of the onset of stress from this component of kraft mill effluent than is blood clotting time. Higher exercise apparently ameliorates the stress effects experienced.

Acknowledgments — We thank H. W. Mahood and I. H. Rogers for preparation of the dehydroabietic acid and J. C. Davis for reading the manuscript.

BLAXHALL, P. C., AND K. W. DAISLEY. 1973. Routine haematological methods for use with fish blood. J. Fish Biol. 5: 771–781.

DAVIS, J. C. 1973. Sublethal effects of bleached kraft pulp mill effluent on respiration and circulation in sockeye salmon (*Oncorhynchus nerka*). J. Fish. Res. Board Can. 30: 369–377.

DAVIS, J. C., AND R. A. W. HOOS. 1975. Use of sodium pentachlorophenate and dehydroabietic acid as reference toxicants for salmonid bioassays. J. Fish. Res. Board Can. 32: 411–416.

DAVIS, J. C., AND B. J. MASON. 1973. Bioassay procedures to evaluate acute toxicity of neutralized bleached kraft pulp mill effluent to Pacific salmon. J. Fish. Res. Board Can. 30: 1565–1573.

GARDNER, G. R., AND P. P. YEVICH. 1969. Studies on the blood morphology of three estuarine cyprinodontiform fishes. J. Fish. Res. Board Can. 26: 433–447.

HALBROOK, N. J., AND R. V. LAWRENCE. 1966. The isolation of dehydroabietic acid from disproportionated rosin. J. Org. Chem. 31: 4246–4247.

HESSER, E. F. 1960. Methods for routine fish haematology. Prog. Fish Cult. 22: 164–171.

KLONTZ, G. W., AND L. S. SMITH. 1968. Methods of using fish as biological research subjects, p. 325–385. *In* W. I. Gay [ed.] Methods of animal experimentation. Vol. III. Academic Press, Inc., New York, N.Y.

KRUZYNSKI, G. M. 1972. Some effects of dietary methoxychlor on brook trout, (*Salvelinus fontinalis*).

M.Sc. Thesis. Sir George Williams Univ., Montreal, Que. 131 p.

LEACH, J. M., AND A. N. THAKORE. 1973a. Identification of the constituents of kraft pulping effluent that are toxic to juvenile coho salmon (*Oncorhynchus kisutch*). J. Fish. Res. Board Can. 30: 479–484.

1973b. Isolation of toxic constituents of kraft pulp mill effluents. CPAR Proj. 11-4. Annual report for the year ending March 31, 1973. Dep. Environ., For. Serv. 37 p.

MCLEAY, D. J. 1970. A histometric investigation of the activity of the pituitary-interrenal axis in juvenile coho salmon, *Oncorhynchus kisutch* Walbaum. Ph.D. Thesis. Univ. British Columbia, Vancouver, B.C. 189 p.

1973a. Effects of a 12-hr and 25-day exposure to kraft pulp mill effluent on the blood and tissues of juvenile coho salmon (*Oncorhynchus kisutch*). J. Fish. Res. Board Can. 30: 395–400.

1973b. Effects of ACTH on the pituitary-interrenal axis and abundance of white blood cell types in juvenile coho salmon, *Oncorhynchus kisutch*. Gen. Comp. Endocrinol. 21: 431–440.

1973c. Effects of cortisol and dexamethasone on the pituitary interrenal axis and abundance of white blood cell types in juvenile coho salmon, *Oncorhynchus kisutch*. Gen. Comp. Endocrinol. 21: 441–450.

MCLEAY, D. J., AND D. A. BROWN. 1975. Effects of acute exposure to bleached kraft pulp mill effluent on carbohydrate metabolism of juvenile coho salmon (*Oncorhynchus kisutch*) during rest and exercise. J. Fish. Res. Board Can. 32: 753–760.

POSTON, H. A. 1964. Effect of dietary vitamin K and sulfaguanidine on blood coagulation time, microhaemotocrit and growth of immature brook trout. Prog. Fish Cult. 26: 59–64.

ROGERS, I. H. 1973. Isolation and chemical identification of toxic components of kraft mill wastes. Pulp Pap. Mag. Can. 74: T303–T308.

ROGERS, I. H., J. C. DAVIS, G. M. KRUZYNSKI, H. W. MAHOOD, J. A. SERVIZI, AND R. W. GORDON. 1975. Fish toxicants in kraft effluents. Tappi 58: 136–140.

SNIESZKO, S. F. 1960. Microhaematocrit as a tool in fishery research and management. U.S. Fish Wildl. Serv., Spec. Sci. Rep.-Fish. 341: 15 p.

WEINREB, E. L. 1958. Studies on the histology and histophathology of the rainbow trout, *Salmo gairdneri irideus*. I. Hematology: under normal and experimental conditions of inflammation. Zoologica (New York) 43: 145–153.

Overhead-Light Intensity and Vertical Positioning of the Walleye, *Stizostedion vitreum vitreum*

E. SCHERER

Department of the Environment, Fisheries and Marine Service, Freshwater Institute, Winnipeg, Man. R3T 2N6

SCHERER, E. 1976. Overhead-light intensity and vertical positioning of the walleye, *Stizostedion vitreum vitreum*. J. Fish. Res. Board Can. 33: 289–292.

Laboratory experiments were devised to test field observations and eye-histological indications that light may strongly influence the spatial distribution of the walleye (*Stizostedion vitreum vitreum*). In 48 tests, fish were exposed to sequences of three different light intensities in discrete logarithmic steps, viz. 200, 20, 2 lx, in that and in reversed order. The result was an inverse relation between light intensity and height of fish position in the test tank, with highly significant differences between positions at different intensities. This response may provide the basis for a useful technique to detect sublethal levels of environmental toxicants.

SCHERER, E. 1976. Overhead-light intensity and vertical positioning of the walleye, *Stizostedion vitreum vitreum*. J. Fish. Res. Board Can. 33: 289–292.

Nous avons monté des expériences de laboratoire dans le but de vérifier des observations sur le terrain et des indications visuelles et histologiques à l'effet que la lumière peut fortement influencer la distribution spatiale du doré (*Stizostedion vitreum vitreum*). Dans 48 essais, les poissons ont été exposés à des successions de trois différentes intensités lumineuses par étapes logarithmiques distinctes, viz. 200, 20 et 2 lux, dans cet ordre et dans l'ordre inverse. Les résultats montrent une relation inverse entre l'intensité lumineuse et la hauteur de position des poissons dans le bassin d'essai, les différences entre les positions à diverses intensités étant hautement significatives. Cette réponse peut servir de base à une technique utile de détection des niveaux sublétaux de toxiques dans l'environnement.

Received August 5, 1975
Accepted November 17, 1975

Reçu le 5 août 1975
Accepté le 17 novembre 1975

Printed in Canada (J3935)
Imprimé au Canada (J3935)

FIELD observations indicate that walleyes (*Stizostedion vitreum vitreum*) avoid high light intensities. These predacious perches are reported to stay in deeper layers of a lake or under shelters during bright hours of the day, but to feed up to the top of the water column at night (e.g. Scott and Crossman 1973). Also, a tapetum lucidum in the walleye's eye, favoring dim-light perception, supports the assumption that light intensity may be a factor influencing the spatial distribution of this species (Ali and Anctil 1968). However, experimental evidence for a causal relation has been lacking so far. Thus, the aim of this study was to test the walleye's response to light under controlled conditions. Furthermore, I tried for a test procedure that is easy to duplicate, so it may be used to detect and quantify the effect of pollutants on the response of a fish to a major environmental factor.

Materials and methods — In a previous paper (Scherer 1971), increase of free CO_2 and decrease of O_2 in the water were shown to cause this species to assume higher vertical positions, even though illumination at the water surface was kept constant at 2400 lx. In the present investigation, light intensity was varied whereas all other conditions were maintained as constant as possible. Although some fluctuations did occur, conditions known to alter the light response (Scherer 1971) were not reached (Table 1). Also, thorough checks revealed no stratification of temperature O_2, CO_2, or pH in the test tank (size 40 $\times 45 \times 90$ cm).

A batch of 78 second-summer walleyes (10–14 cm long) was used for these tests. Originating from a provincial hatchery at Lake Manitoba, these fish lived during their first summer in one of the Freshwater Institute's fish farming lakes, and were kept thereafter in laboratory tanks at 15 C, the designated test temperature. A daily cycle of 12 h darkness and 12 h illumination was maintained in the holding area (LD 12:12 [7:00–19:00]). The fish were fed daily between 8:30 and 9:00 with frozen brine shrimp ad libitum. Tests were done one per day, always in the afternoon, in series of 12 on consecutive days (except weekends). The whole investigation stretched over 5 mo.

After transfer of three randomly selected specimens to the test tank, fish were given 2 h for habituation and for adaptation to 200 lx before testing commenced. A fixed sequence of light intensities was presented in each test: 200, 20, 2, 2, 20, 200 lx as measured directly under the glass bottom of the tank (Table 2). Each light phase lasted exactly 15 min. In conjunction with Luxtrol® dimmers, Vitalite® fluorescent bulbs were chosen for their good daylight-simulating spectral energy distribution (color rendering index $R_a = 0.91$ at 5500 K). Spectral changes through dimming were not noticeable to the human eye, nor substantiated by spectroradiometric measurements. During tests, the vertical positions of three fish at a time were recorded manually every 10 s, using a time-giving earphone, and a grid at the front plate of the aquarium marking 13 equal layers over 39 cm of total water column. Five minutes were left unrecorded between each change of light intensity; this interval proved sufficient to let fish quiet down after some excitation occasionally observed during and immediately after changing the light, or after removing and reinstalling the one-way mirror between tank and experimenter before and after the 2-lx levels. The latter procedure was necessary because the fish were not clearly visible behind the mirror at this low intensity. The experimenter sat as quietly and as motionless as possible during these 2-lx phases; as always, no illumination other than that emanating from the tank was provided. There was no indication of fish reacting to the observer in that situation.

The four replicate series (a–d) yielded 48 tests with a total of 77,760 position recordings, or 12,960 recordings per light phase (three fish $\times$ 6 recordings per minute $\times$ 15 min per light phase $\times$ 48).

Results — Results from each of the four replicates (Fig. 1) show a consistent inverse relation between overhead-light intensity and vertical position of the fish.

Two response features emerged as characteristic:

1) Within the given stimulus sequence, responses were largest (as indicated by net difference in vertical position) when light changed from 20 to 2 and from 2 to 20 lx, in all four test series.

2) During the second 2-lx phase, the fish always moved higher than during the first. This rise through adaptation and/or habituation (see discussion) was carried over to some extent to

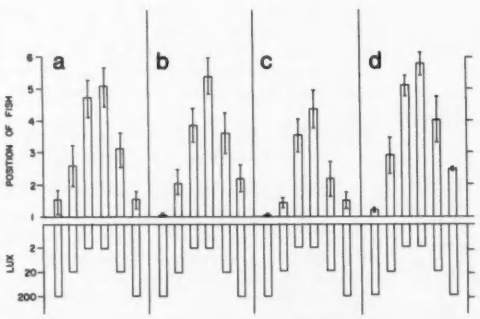

FIG. 1. Vertical positions of walleyes (*Stizostedion vitreum vitreum*) at three different light intensities presented in a fixed sequence. Columns indicate means with standard errors ($n = 12$) of vertical positions attained. Four replicate test series (*a–d*).

TABLE 1. Experimental conditions, test series *a* to *d* ($\bar{x} \pm s_{\bar{x}}$)

	CO_2		O_2		
	mg/liter	mm Hg	mg/liter	pH	Temp C
a	2.14±0.27	0.81±0.10	9.8±0.26	7.8±0.1	15.2±0.4
b	1.10±0.23	0.42±0.09	9.5±0.23	8.1±0.1	15.0±0.3
c	1.36±0.20	0.51±0.08	9.1±0.16	8.1±0.1	15.4±0.5
d	1.14±0.26	0.43±0.10	9.1±0.20	8.1±0.1	15.3±0.3

TABLE 2. Light intensities (lx), at upper limits of positions 1–6, and at ~ 2 mm beneath water surface, measured along the water column above light cell (= reference point). In parentheses: ranges observed in three profiles laid through tank, providing eight columns additional to the one above reference point.

Surface	4.4	46	355
	(3.5 –4.74)	(31.8–46)	(275–355)
6	3.28	32	275
	(2.73–3.75)	(22.4–33.8)	(228–285)
5	3.15	30	267
	(2.65–3.65)	(21.8–39.5)	(225–278)
4	3.0	29	258
	(2.65–3.5)	(21 –38.7)	(222–270)
3	2.9	28.5	250
	(2.4 –3.36)	(20 –38.4)	(217–260)
2	2.7	25	245
	(2.31–3.27)	(20.8–37.6)	(221–267)
1	2.6	25	245
	(2.18–3.32)	(21.8–36.7)	(215–259)
Tank bottom	2	20	200

the last two light phases, so that for each of the series a–d, the sum of mean positions during the last two light phases was larger than during the first 200 and 20 lx.

Figure 2 compiles the results of all 48 experiments; statistical tests on these data (Student's *t*, one-tailed) yielded highly significant differences in fish position for all different light intensities ($P < 0.001$). Exponential curves fitting the data points were derived from the regression analysis program of a desk computer (HP 9100B, Stat Pac X-10).

Observed, though not quantitatively recorded, were conspicuous and consistent changes in locomotor activity during the course of each test. During the initial 200 lx, the fish would move very little, horizontally or vertically; in some experiments they actually rested motionless for the entire 15 min. At 20, and again at 2 lx, general locomotor activity (i.e. rate of horizontally as well as vertically oriented movements) increased noticeably. During the last two light intensities activity waned again. It was the exception rather than the rule, however, to see all three test-specimens as inactive at the end of the test as they typically were at the beginning (see Discussion).

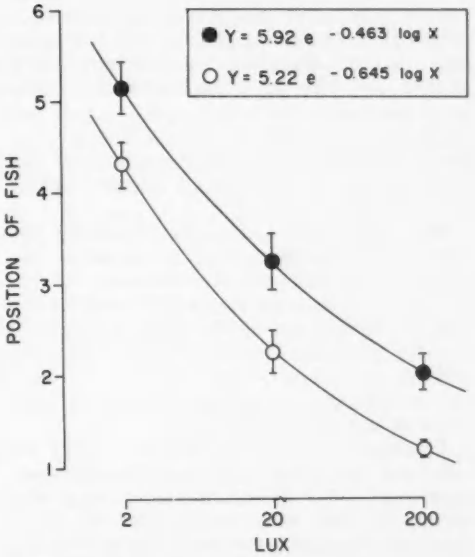

FIG. 2. Vertical positions of walleyes at three different light intensities presented in a fixed sequence. Data points represent means of all experiments with standard errors ($n = 48$). Open circles, first half of test schedule, from 200 to 2 lx. Closed circles, second half of test schedule, from 2 to 200 lx.

Correlated with changes of activity were changes in body coloration; fish were an overall pale color when active (in lower as well as upper layers of the tank); a generally darker integument and distinctive dark bars on the sides of the body were observed as long as the fish were motionless or moved but little.

Discussion — The present results demonstrate two main points: 1) Changes in overhead-light

intensity alone elicit vertical movements in the same directions as observed in the field where light is linked to several other vertically dishomogeneous and diurnally fluctuating factors; 2) The test procedure reported here leads to well reproducible response quantifications.

The latter point is noteworthy in view of the high level of integration underlying the recorded response, from light perception and intensity discrimination via eyes (and, possibly, pineal and skin) to locomotor output. Physiological impairment at any site within this system can be expected to change the response pattern. This suggests that the technique reported here can be applied for detecting effects of environmental toxicants. Indeed, in a first series of such sublethal assays a significant response reduction was found in walleyes that had accumulated high mercury concentrations through ingestion (Scherer et al. 1976).

The marked shift to higher mean vertical positions during the second half of the test as compared to the first can be understood to result from sensory adaptation and behavioral habituation; further, a photokinetic effect contributed in that the increase in locomotor activity (including vertical movements) from 200 to 2 lx waned only slowly and incompletely during the subsequent 20 and 200 lx phases.

Woodhead (1966) and Blaxter (1970) provided the most recent literature reviews on reactions to light and vertical migration of fish, dealing mainly with field investigations. It appears that light intensity is a principal factor in controlling or triggering vertical movements in most species (best documented for the herring; data on walleye or closely related species not available so far). Both authors, however, emphasize the modifying influence of other factors, biotic (e.g. movements of prey, endogenous activity patterns) and abiotic (e.g. the gradient of static pressure, stratification of temperature, oxygen). In no case have such interactions been quantitatively elucidated; nevertheless, their existence and importance also for the walleye is likely. Factorial experiments and multivariate analysis of field data appear necessary as the next step in understanding the vertical distribution of *Stizostedion vitreum vitreum.*

Acknowledgments — Miss J. McIntosh and Mr S. H. Nowak assisted ably in experiments and data processing. For helpful comments on the manuscript I thank Drs J. H. Gee, F. J. Ward (both University of Manitoba), and R. R. Wallace (Freshwater Institute).

ALI, M. A., AND M. ANCTIL. 1968. Corrélation entre la structure rétinienne et l'habitat chez *Stizostedion vitreum vitreum* et S. canadense. J. Fish. Res. Board Can. 25: 2001–2003.

BLAXTER, J. H. S. 1970. Light — Fishes, p. 213–320. *In* O. Kinne [ed.] Marine ecology. Vol. I, Pt. 1. Wiley-Interscience, London, New York, Sydney, Toronto.

SCHERER, E. 1971. Effects of oxygen depletion and carbon dioxide buildup on the photic behaviour of the walleye (*Stizostedion vitreum vitreum*). J. Fish. Res. Board Can. 28: 1303–1307.

SCHERER, E., F. A. J. ARMSTRONG, AND S. H. NOWAK. 1976. Effects of mercury-contaminated diet upon walleyes, *Stizostedion vitreum vitreum*. Fish. Mar. Serv. Res. Dev. Tech. Rep. No. 597: 21 p.

SCOTT, W. B., and E. J. CROSSMAN. 1973. Freshwater fishes of Canada. Bull. Fish. Res. Board Can. 184: 966 p.

WOODHEAD, P. M. J. 1966. The behaviour of fish in relation to light in the sea. Oceanogr. Mar. Biol. Annu. Rev. 4: 337–403.

Low Thermal Responsiveness in the Bluegill, *Lepomis macrochirus*

THOMAS L. BEITINGER[1] AND JOHN J. MAGNUSON

Laboratory of Limnology, Department of Zoology, The University of Wisconsin-Madison, Madison, Wis. 53706, USA

BEITINGER, T. L., AND J. J. MAGNUSON. 1976. Low thermal responsiveness in the bluegill, *Lepomis macrochirus*. J. Fish. Res. Board Can. 33: 293–295.

Fifteen young bluegill, *Lepomis macrochirus*, acclimated to 5 C for at least 1 mo, died during temperature preference testing owing to apparent voluntary exposure to high temperatures. The mortality rate of 100% for these fish greatly exceeded the 3.8% rate found for 262 bluegill acclimated to temperatures ranging from 20 to 34 C, and tested in the same apparatus. Modifications in the experimental design whereby fish acclimated to 5 C were held at about 19 C for 24 h during testing, enabled all fish to survive. These bluegill selected temperatures only 2 C lower than those acclimated to summer conditions.

BEITINGER, T. L., AND J. J. MAGNUSON. 1976. Low thermal responsiveness in the bluegill, *Lepomis macrochirus*. J. Fish. Res. Board Can. 33: 293–295.

Quinze crapets arlequins, *Lepomis macrochirus*, acclimatés à 5 C durant au moins 1 mois, moururent lors d'essais sur la température préférée à la suite d'une exposition apparamment volontaire à de hautes températures. Ce taux de mortalité de 100% dépasse de beaucoup celui de 3.8% observé chez 262 crapets arlequins acclimatés à des températures allant de 20 à 34 C et soumis à des essais dans le même appareil. Des modifications au protocole expérimental selon lesquelles les poissons acclimatés à 5 C furent maintenus à environ 19 C durant 24 h pendant l'essai permirent à tous les poissons de survivre. Ces derniers choisirent des températures de seulement 2 C inférieures à leur température préférée d'été.

Received July 11, 1975
Accepted October 14, 1975

Reçu le 11 juillet 1975
Accepté le 14 octobre 1975

PECULIAR behavior and mortality of warmwater fish species acclimated to low temperatures have been observed previously. In laboratory experiments with opaleye, *Girella nigricans*, Norris (1963) found that the reactions of cold-acclimated fish to thermal gradients appeared dulled. Opaleye often remained at temperatures usually avoided. Underyearling white bass (*Morone chrysops*), yellow perch (*Perca flavescens*), and adult smallmouth bass (*Micropterus dolomieui*) captured during fall and winter and given access to a laboratory temperature gradient explored beyond their critical thermal maxima and died (Barans and Tubb 1973). Similar inability of young white perch (*Morone americana*) and striped bass (*M. saxatilis*) to avoid stressful or even lethal temperatures while in thermal gradient has been termed "low thermal responsiveness" by Meldrim and Gift (1971). This paper reports an occurrence of low thermal responsiveness in the bluegill, *Lepomis macrochirus*.

[1]Present address: Radiological and Environmental Research Division, Argonne National Laboratory, Argonne, Ill. 60439, USA.

Printed in Canada (J3904)
Imprimé au Canada (J3904)

Materials and Methods — Bluegill (mean ± SD = 90.5 ± 10.4 mm TL) captured from Lake Wingra (Dane County, Wisconsin) were held in the laboratory at 5 C and photoperiods of either LD 9:15 (i.e. light–dark) or LD 15:9 for at least 4 wk prior to experiments.

The temperature preference apparatus was similar in design to that of Neill et al. (1972) with modifications reported by Beitinger et al. (1975). Each 50-liter test tank (60 cm × 28 cm × 29 cm) was divided into halves by a fiberglass partition. A tunnel (~5 cm diam) in the partition allowed the fish access to the two halves which differed by a fixed 2 C. Passage of a fish into the warmer tank half caused the temperature of the entire tank to increase 3.0 C/h, and both halves decreased at the same rate when the fish moved into the cooler half. At all times the 2 C differential was maintained between tank halves. A lower limit of 4 C was maintained in the cooler half of each tank. When the temperature in the cooler tank equaled this limit, temperatures remained constant (4 C cool side: 6 C warm side) until the fish again entered the warmer half. Because it was difficult to maintain temperatures less that 4.0 C, this precaution insured close agreement between thermostatic setting and actual tank temperature when fish were selecting low temperatures.

Individual fish, acclimated to 5 C, were placed in preference tanks at constant temperatures 1 C below and 1 C above their acclimation temperature for 2.5

days. In the initial trial, usual procedures (Beitinger et al. 1975) were employed, i.e. following the 2.5 preexperimental period, tank temperature control was relinquished to each fish. In the second trial, modifications were performed in an attempt to avert the mortalities seen in trial 1. As individual fish increased the warmer tank temperature to 18–20 C, the temperature rate-change mechanism was disengaged and temperatures were held constant. After 24 h, rate-change was reinstituted returning control of tank temperature to the fish. The preferred temperature for each fish was assessed from data collected during the 3-day period following reinstitution of temperature rate change. Photoperiods during experimentation were consistent with those during acclimation. Pelleted food was presented to each fish daily at 1400 h ± 15 min.

Results and discussion — During the 2.5-day, temperature-static period, bluegill spent the majority of their time (median = 81.8%; interquartile range = 62.5–94.7%) in the warmer (6.0 C) tank half. When given control over tank temperatures, fish remained in the warmer half causing tank temperatures to increase. Fish appeared sluggish, unresponsive, and did not accept food pellets. In two trials of five fish each, all bluegill acclimated to 5 C and LD 15:9 died. Similarly, five of five fish acclimated to 5 C and LD 9:15 also died during testing. Most mortalities occurred during the first experimental night at tank temperatures of 18–30 C. None of these fish survived longer than 49 h. The temperature range at which death occurred includes the range of upper lethal temperatures for bluegill acclimated to 5 C (Speakman and Krenkal 1971). The 100% mortality rate observed in 5C-acclimated bluegill was completely unexpected since an apparent "voluntary"[2] mortality rate of only 3.8% (10/262) was found in the same preference tanks for fish acclimated from 20 to 34 C. Fully 67% (10/15) of the dead fish were found in the warmer tank half. These fish were either "ignorant" of the cooler temperatures in the alternate tank half, unable to find or enter the cooler half, or were attempting to reach temperatures in the vicinity of their final preferendum (~31 C). Of the numerous environmental factors and experimental manipulations imposed on fish in our temperature preference research (see Beitinger 1974), only acclimation to 5 C resulted in nonconservative behavior by test fish.

In Meldrim and Gift's (1971) report of low thermal responsiveness, only the smallest fish suffered mortalities. Conceivably, larger fish that explored high temperatures had sufficient time to escape thermal death owing to the size-related latency in equilibrium of body temperatures with ambient temperatures. In experiments reported here, "escape" from potentially lethal high temperatures was limited by the relatively slow (3.0 C/h) rate of temperature decrease. These findings suggest that 5 C-acclimated bluegill are attracted to temperatures at which they cannot survive owing to their low thermal acclimation state.

The second trial of bluegill acclimated to 5 C and LD 9:15 was modified to determine whether or not short-term exposure to higher temperatures would affect low thermal responsiveness. Utilizing this procedure all five fish survived, generating a median preferred temperature of 29.2 C, encompassed by an interquartile range of 26.6–29.9 C. The 24-h experimental "hiatus" apparently allowed fish sufficient time to increase their thermal acclimation state, thereby permitting survival at temperatures approaching their final preferendum. The median preferred temperature of these fish was about 2 C lower than bluegill acclimated to temperatures above 20 C.

Two hypotheses are offered to account for the low thermal responsiveness exhibited by winter-acclimated bluegill in these experiments. One, fish were seeking their final preferendum, i.e. their behavior was normal, but the rapid increase in tank temperature exceeded the physiological and biochemical capacities to adjust, hence death ensued. Two, a behavioral dysfunction occurred as a result of introducing fish into temperature gradients that were inconsistent with their thermal acclimation states. Although experimental manipulations in the last trial intimated the involvement of acclimation processes, this evidence does not eliminate either hypothesis.

Regardless of the underlying mechanism, the behavioral responses of winter-acclimated bluegill in these experiments were clearly nonconservative.

Acknowledgments — We greatly appreciate the technical assistance of W. R. Shaffer, S. A. Klinger, and G. D. Chipman of the University of Wisconsin's Laboratory of Limnology. We thank Dr S. A. Spigarelli for his review of the manuscript. Ms P. Tyrolt assisted in the preparation of the manuscript. This paper resulted from studies supported by research grants to Dr Magnuson from the Madison Gas and Electric Company and the National Oceanic and Atmospheric Administration's Office of Sea Grant (Department of Commerce) through an institutional grant to the University of Wisconsin.

[2]In this system, mortalities could be traced to the following: electronic failure (>75% of all mortalities), biological (behavioral) failure, or undetermined. The reported 3.8% mortality rate is the sum of the latter two.

BARANS, C. A., AND R. A. TUBB. 1973. Temperatures selected seasonally by four fishes from western Lake Erie. J. Fish. Res. Board Can. 30: 1697–1703.

BEITINGER, T. L. 1974. Influence of abiotic and biotic factors on the stability of behavioral termogregulation in fishes, particularly the bluegill. Ph.D. Thesis. Univ. Wisconsin-Madison, Madison, Wis. 240 p.

BEITINGER, T. L., J. J. MAGNUSON, W. H. NEILL, AND W. R. SHAFFER. 1975. Behavioral thermoregulation and activity patterns in the green sunfish, *Lepomis cyanellus*. Anim. Behav. 23: 203–210.

MELDRIM, J. W., AND J. J. GIFT. 1971. Temperature preference, avoidance and shock experiments with estuarine fishes. Ichthyol. Assoc. Bull. 7: 75 p.

NEILL, W. H., J. J. MAGNUSON, AND G. D. CHIPMAN. 1972. Behavioral thermoregulation by fishes: a new experimental approach. Science 176: 1443–1445.

NORRIS, K. S. 1963. The function of temperature in the ecology of the percoid fish, *Girella nigricans*. Ecol. Monogr. 33: 23–62.

SPEAKMAN, J. N., and P. A. KRENKEL. 1971. Quantification of the effects of rate of temperature change on aquatic biota. Dep. Environ. Water Res. Eng., Vanderbilt Univ., Nashville, Tenn. 6: 178 p.

Dr Fry during the discussions. (Photograph by S. Griffith.)

PERSPECTIVES

Natura Naturans: A Symposium on the Fry Paradigm

The proceedings of a Symposium held at the Harkness Laboratory of Fisheries Research, Algonquin Park, Ontario, on October 8–10, 1974, in honor of Professor F.E.J. Fry, M.B.E., M.A., Ph.D., D.Sc., F.R.S.C.

EDITED BY S. R. KERR AND A. H. LAWRIE

Ontario Ministry of Natural Resources, Maple, Ont.

Contents

INTRODUCTION 298–299

SELECTED PAPERS

Some concepts and descriptions of physiological tolerance: rate–temperature curves of poikilotherms as transects of response surfaces **D. F. Alderdice** 299–307

Scope for metabolism and growth of sockeye salmon, *Oncorhynchus nerka*, and some related energetics **J. R. Brett** 307–313

Predation, yield, and ecological efficiency in aquatic food chains **L. M. Dickie** 313–316

Selective breeding and hybridization in fisheries management **P. Ihssen** 316–321

A new approach to fisheries management and F. E. J. Fry's role in its development **K. H. Loftus** 321–325

Initiation of sea lamprey control **W. M. Sprules** 326–329

Ecological analysis and the Fry paradigm **S. R. Kerr** 329–332

Comments 332–335

SELECTED EXCERPTS FROM SYMPOSIUM DISCUSSION PERIODS 337–339

ACKNOWLEDGMENTS 339

PROFILE OF F. E. J. FRY 340–344

LIST OF PARTICIPANTS 344–345

Printed in Canada (J4029)
Imprimé au Canada (J4029)

Introduction

SUBSTANTIAL progress in any scientific discipline is essentially and inescapably an expression of personal creativity. The history of science is replete with individuals who, whatever the vicissitudes of what passed for "science policy" in their times, importantly shaped the development of their science.

"Good" science is therefore an intensely personal but not necessarily lonely activity. Indeed, if the creative individual also offers sufficient stimulus, guidance, and personal magnetism to shape and channel the activities of his students and colleagues, then a new scientific school or movement can result.

If sufficiently radical and comprehensive, the Weltanschauung afforded by such a creative individual can constitute a conceptual outlook, or paradigm in the general sense offered by Thomas Kuhn (1970): a redirection of activity that considerably shapes the "conventional science" that is its aftermath.

The proceedings reported here reflect a collective effort to define and elaborate the substance of such a paradigm. What follows is an account of a symposium held late in 1974, on the theme of the Fry Paradigm: the conceptual outlook conferred on ecological science by F. E. J. Fry. The motivation, or excuse, was to mark the occasion of Dr Fry's formal retirement from the Department of Zoology of the University of Toronto. Judged by Dr Fry's subsequent commitments and activities, the retirement, happily, was highly illusory and, therefore, a matter of little present consequence (see Profile).

The title chosen for the Symposium, "Natura Naturans" (literally, "nature naturing") is a term borrowed from the medieval philosophers, who used it to connote an integral appreciation of nature in all its complexity. As these proceedings will show, the titular choice was apposite.

Although in the nature of a Festschrift, these proceedings hopefully represent something more than the usual collection of relatively unconnected contributions by students and colleagues. A deliberate effort was made, through invitations to representative contributors, to capture the essentials of the Fry paradigm in its manifold realizations in autecology, synecology, applied ecology, and philosophy of science. Those who were fortunate enough to participate in the Symposium itself have little doubt of the measure of success that was achieved. The physical environment afforded by the Harkness Laboratory, and the intellectual environment provided by those in attendance, conspired to assure success. What is less certain is that the experience enjoyed by those in attendance can be abridged and adequately captured in print.

A brief description of the format of the Symposium is in order. A priori, the organizers were faced with a dilemma. The basic strategy was to assemble a small, representative group of Fry associates in an informal setting that would promote easy discussion of a loosely structured series of themes. Granted the magnitude of Dr Fry's influence on the present generations in aquatic science, selection of participants was no easy task: the invitation list was in fact highly arbitrary except that each category and generation of Fry's major scientific interests was represented by at least one person. Similarly, it was not easy to select a series of discussion themes that adequately captured the varied attributes of a multifaceted scientific campaign within the serial constraint of a symposium format.

The various contributors were asked to come prepared either to present a short, succinct review paper elucidating Dr Fry's contributions to a particular theme, or alternatively, to serve as a discussant for one or more of the themes. Those who were to contribute a paper were not constrained by a publication requirement: but the fact that some papers at least would be publishable was recognized. These contributors were given the option of including their paper in this account of the Symposium. The papers that follow, therefore, constitute an incomplete but representative sampling of the more formal portions of the proceedings.

The spoken proceedings were recorded on magnetic tape. Some particularly interesting portions of this record, spoken in large part by Dr Fry, were edited somewhat but otherwise reproduced verbatim in what follows. The tapes themselves have been deposited in the Research Library of the Ontario Ministry of Natural Resources.

Selected Papers

The various papers presented to the Symposium were all of substantial quality. The sole criterion applied to their reproduction here was whether they possessed sufficient new content to justify publication for a general audience: this is entirely a reflection of the constraints imposed upon the authors by the organizing committee. It does not imply that the following were by any means the "best" papers contributed. It does say that each was judged to contain more in the way of new insight than could be adequately conveyed in a summary of the proceedings.

The influences of external agencies upon the functional responses of biological entities are pivotal to an understanding of the Fry paradigm.

The three papers by Alderdice, Brett, and Dickie deal with different aspects of this central theme. Taken together, they illustrate the pervasive effects of the theoretical issues first extensively developed in Fry's well-known 1947 monograph "Effects of the environment on animal activity."

Less obviously, perhaps, the fundamental internal processes that underlie the patterns of organismic response to external factors are equally central to the Fry paradigm. Most fundamental of all, in this respect, are the genetic processes which underwrite such responses. The paper by Ihssen represents this component of the paradigm. It is exceptional to the editor's criterion for inclusion here, however, in the sense that the material reviewed by Dr Ihssen is not new to science: it is generally new, however, to that majority of readers who are not abreast of current theory in population genetics, and serves admirably to illustrate this important dimension of Dr Fry's interests.

All who know him are abundantly aware of Dr Fry's practical bent. Whether it takes the form of oxygen breathing apparatus, plastic greenhouses, solar power, or, less unexpectedly, management measures for fisheries resources, the Fry paradigm has been realized in a multitude of utilitarian ways (and an equivalent number of proven impracticalities — such is the well-known resourcefulness of the man!) The papers by Loftus and Sprules reflect two substantial (and utilitarian) aspects of the paradigm.

To this point, the "Fry Paradigm" has been referred to as if it were something as clearly defined as say, the "thermal zone of tolerance." It is not. Neither, as with any complex phenomenon, does it present itself with the ease and clarity of some comportable aphorism. It is just as difficult to get at as anything else worthwhile. The final paper, by Kerr, attempts to provide us with a glimmering. Of greater importance than the paper itself is the response it elicited from Dr Fry, which is reproduced, in slightly edited form, following the paper.

Some Concepts and Descriptions of Physiological Tolerance: Rate–Temperature Curves of Poikilotherms as Transects of Response Surfaces[1]

D. F. ALDERDICE

Department of the Environment, Fisheries and Marine Service, Pacific Biological Station, Nanaimo, B.C.

ALDERDICE, D. F. 1976. Some concepts and descriptions of physiological tolerance: rate–temperature curves of poikilotherms as transects of response surfaces. J. Fish. Res. Board Can. 33: 299–307.

Precht rate curves may be considered as transects across a rate surface bounded by a Fry temperature polygon. Changes in metabolic or active capacity within the tolerance polygon approximate capacity changes within Precht's normal range of temperatures. Precht's resistance adaptations are consequences of change in capacity occurring in the zone of resistance of Fry.

The turning-point axis of Precht rate curves is assumed analogous to the axis of maximum rate at acute temperatures (test-temperature axis), using an activity surface as a model. Parallelism is suggested between this axis and the upper incipient lethal temperature boundary where the latter may be unknown.

In the standard comparison of cold-adapted and warm-adapted rates, Precht compensation types can depend on the nature of the capacity surface and on the choice of acclimation temperatures. Reasonable and paradoxical resistance adaptations reflect characteristics of the capacity surface, in particular the turning-point axis, in relation to the acclimation and acute temperature axes of measurement. Resistance adaptations appear directly related to the course of the incipient lethal boundaries on a rate surface. Further understanding of capacity surfaces

[1]This paper forms part of the proceedings of a Symposium convened at the Harkness Laboratory of Fisheries Research, Algonquin Park, Ontario, October 1974, in honor of Professor F. E. J. Fry, M.B.E., M.A., Ph.D., D.Sc., F.R.S.C.

Printed in Canada (J4030)
Imprimé au Canada (J4030)

probably requires that a minimum of five transects be made across a surface, rather than the two generally made for warm-adapted and cold-adapted comparisons.

In such studies, meaningful measures of acute response require extended understanding of the nature and time course of thermal acclimation, and of the potential biases embedded in a response arising from other temperature-dependent compartments of metabolic demand. The need is demonstrated for a quantitative distinction between thermal resistance and tolerance in cells and microorganisms, equivalent to the incipient lethal temperature boundaries of Fry. Such determinations, above all, require that temperature level and exposure time not be confounded.

ALDERDICE, D. F. 1976. Some concepts and descriptions of physiological tolerance: rate–temperature curves of poikilotherms as transects of response surfaces. J. Fish. Res. Board Can. 33: 299–307.

Les courbes de taux de Pretch peuvent être considérées comme des transversales à travers une surface de taux comprise dans les limites d'un polygone de température de Fry. Les variations de capacité métabolique ou active, dans les limites du polygone de tolérance, se rapprochent des variations de capacité dans la gamme normale de température de Pretch. Les adaptations de résistance de Pretch sont une conséquence du changement de capacité se produisant dans la zone de résistance de Fry.

On suppose que l'axe du point de tour des courbes de Pretch est analogue à l'axe de taux maximal à des températures aiguës (axe de température d'essai), utilisant une surface d'activité comme modèle. On suggère un parallélisme entre cet axe et la limite supérieure de température de début des mortalités dans les cas où cette limite est inconnue.

Dans une comparaison conventionnelle des taux chez des individus adaptés au froid et à la chaleur, les types de compensation de Pretch peuvent dépendre de la nature de la surface de capacité et du choix des températures d'acclimatation. Les adaptations raisonnables et paradoxales de résistance reflètent les caractéristiques de la surface de capacité, en particulier l'axe du point de tour, en rapport avec les axes de mesure de la température d'acclimatation et de la température aiguë. Les adaptations de résistance semblent directement liées à la direction des frontières marquant le début des mortalités sur une surface de taux. Une meilleure compréhension des surfaces de capacité exige probablement un minimum de cinq transversales à travers une surface, plutôt que les deux ordinairement tracées lors de comparaisons entre des individus adaptés à la chaleur et au froid.

Dans des études de ce genre, les mesures de réponse aiguë, pour être significatives, présupposent une bonne compréhension de la nature et de l'évolution dans le temps de l'acclimatation thermique, et des biais inhérents à une réponse provoquée par d'autres composantes, également dépendantes de la température, de la demande métabolique. L'auteur fait ressortir le besoin d'une distinction quantitative entre la résistance et la tolérance thermique dans les cellules et les microrganismes, équivalant aux frontières de température de début des mortalités de Fry. De telles déterminations exigent avant tout qu'on ne confonde pas niveau de température et temps d'exposition.

Accepted October 28, 1975 Accepté le 28 octobre 1975

IN a recent review (Alderdice 1972; p. 1673 et seq.), concepts of temperature adaptation in poikilotherms, developed by Fry (Fry 1947, 1971; Fry and Hochachka 1970) and by Precht (Precht 1949, 1958, 1964, 1968; Christophersen and Precht 1953; Christophersen 1967), were discussed in relation to response surface analysis. Of the two schools of thought, that of Fry and coworkers has dealt primarily with responses of intact organisms. Precht and his colleagues have worked principally with metabolic responses of organs, tissues, cells, and microorganisms. Common to both schools have been studies of respiratory metabolism as influenced by temperature.

As defined and described, the two concepts appear superficially to be distinct. However, further examination indicates that they are based on the same strategem. This paper attempts to focus attention on the stratagem by reviewing similarities and apparent differences between the two concepts, and problems of interpretation common to both.

Background and Definitions

Poikilotherms essentially are temperature conformers; temperature governs the rate of biochemical reactions, hence the metabolic rate, and thence activities mediated through the effects of temperature on metabolism. *Metabolism* is taken as the sum of the reactions yielding energy the organism utilizes, while *activities* are those things the organism does with the energy derived from metabolism (Fry 1971). Traditionally, metab-

olism has been measured in terms of oxygen consumption. Locomotor performance, on the other hand, is a commonly measured activity.

However, the distinction between metabolism and activity is often a fine one, leading to problems of interpretation. Heart beat and respiration often have served as determiners of metabolic rate. If metabolism is confined to the cellular and subcellular level, then heart beat and respiration are activities associated with transport and delivery of the components of and energy derived from metabolic processes. Nevertheless, such activities may be used as estimators of total metabolism, recognizing that the various compartments contributing to the total may not be strictly comparable from one organism or circumstance to another.

In recent years increased attention has been directed toward determining the contribution of various biological processes to energy utilization. These processes involve the more subtle activities such as growth, respiration, random activity, excretion, digestion, and ion and osmoregulation. In intact higher organisms, both metabolism and activity also may be affected by function of the central nervous system (e.g. excitement metabolism) and hormonal influences (e.g. seasonal effects). Many of these activities can affect measured rates in tissues, cells and microorganisms, as well as in higher organisms. Their control, as variables, leads to more exact descriptions of measured rate processes. Fry and Hochachka (1970, fig. 4) distinguish between *standard*, *routine*, and *active* metabolism, where a measure of control is exercised over locomotor and spontaneous activity and excitement metabolism.

Poikilotherms in general alter rate functions in response to temperature change. The time course of change in response may occur in three phases. There may be an immediate sensory or shock reaction involving *overshoots* or *undershoots* of rate, whose duration is measured in minutes (Grainger 1958, 1960). There may follow a period of altered and essentially stabilized rate whose duration would be measured in hours. Subsequently, a slow change can occur until a new equilibrium is reached after a period of days or weeks (Prosser 1958). The terms adaptation and acclimation will be used more or less interchangeably for this process. *Adaptation* is considered as the alteration of response of an organism of survival value in a changed environment (Prosser 1958). *Acclimation* can be taken as the process by which a new steady state of rate functions is achieved after environmental alteration. In terms of either activity or metabolism, when a response is measured in the temporary phase of rate stabilization, the rates are termed *acute*, signifying that they were obtained before the organism could acclimate to a new level of environmental conditions.

The Fry Concept

Fry (1971) has classified environmental factors in terms of their lethal, controlling, limiting, masking, and directive influences. Comment will be limited to the first three of these classes. Recalling the distinction made between metabolism and activity, temperature is assumed to act as a *lethal* factor primarily by disrupting integrated metabolism. The *temperature tolerance* polygon (Fry *et al.* 1942) provides a quantitative means of distinguishing between *thermal tolerance* and *thermal resistance*. It encloses those combinations of acute and acclimated temperature experience that an organism can tolerate indefinitely (Fig. 1). Conversely, outside the tolerance polygon, temperature experience alone ultimately is lethal.

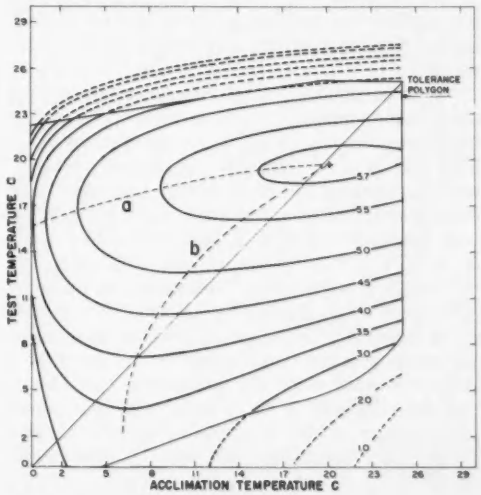

FIG. 1. Influence of acclimation temperature on the critical swimming speed of coho salmon (*Oncorhynchus kisutch*) juveniles, measured acutely at various temperatures. Isopleths of swimming speed (fish lengths per second) are shown inside the tolerance polygon as defined by Brett (1952). Computed maximum swimming speeds occur on "ridges" on the surface, with respect to (a) test or acute temperature (test-temperature ridge), and (b) acclimation temperature. Both ridges culminate in a locus of ultimate maximum swimming speed at the center of the surface. The diagonal line joins equal acclimation and test temperatures. Computed swimming speed isopleths in the zone of resistance are indicated by the broken lines (Griffiths and Alderdice 1972).

Forming the boundaries of the *zone of tolerance* are the *upper* and *lower incipient lethal* temperatures. In the *zone of resistance*, therefore, survival is a function of temperature level and duration of exposure; that is, the *effective time* is the duration of exposure, at a given temperature in the zone of resistance, required to produce the lethal effect.

Rates of activity, measured acutely, may reach a maximum within the zone of tolerance. For example, critical (estimated maximum sustained) swimming speeds of coho salmon juveniles (Griffiths and Alderdice 1972) are maximized on two temperature ridges that culminate in a center for ultimate maximum critical swimming performance near 20 C (Fig. 1). On any selected acclimation temperature transect of the performance surface, within the tolerance polygon, swimming rate is maximized on the upper ridge (a). Below the ridge, temperature appears to act as a controlling factor, governing supply of metabolites and, consequently, the availability of energy for activity. Above the ridge performance declines, suggesting that activity is increasingly dominated by a limiting factor such as progressive restriction of oxygen supply.

Acute determinations of metabolic rate, on the other hand, present other problems. In higher organisms the reason is, of course, the considerable difficulty of making meaningful measurements, unbiased by metabolism associated with sensory stimulation and random activity (Peterson and Anderson 1969; Fry and Hochachka 1970, p. 88; Fry 1971, p. 82 et seq.). In cells and microorganisms similar biases can be present, associated with availability of substrate metabolites, rates of growth, and differences in motility. However, it seems reasonable to expect that a better knowledge of the effects of such biases will be obtained in the future and that closer investigation of the time course of rate changes under acute conditions will assist in this understanding.

The Precht Concept

Precht evolved a classification of adaptation phenomena based on the effects of temperature change on metabolic parameters, particularly in cells, tissues, and microorganisms (Precht 1949, 1964, 1968; Christophersen and Precht 1953). Precht distinguishes between two types of temperature-induced adaptations: those occurring at temperatures within the *normal range (capacity adaptation)*, and those at *temperature extremes (resistance adaptations)*.

Capacity adaptation (performance adaptation, compensation) typically is measured as the difference in magnitude of adapted response at two temperatures (e.g. warm, cold), usually 10 C apart (Fig. 2). Sets of *rate curves* may be generated between those temperatures (t_1, t_2) as follows. Starting with measurement of the adapted response at the lower temperature (t_1), temperature is increased at intervals, the response being measured acutely at each interval up to t_2 (*cold-adapted* rate curve). Similarly, starting with measurement of adapted response at the higher temperature (t_2), the response is measured acutely as the temperature is decreased in steps down to t_1 (*warm-adapted* rate curve). Rate compensation curves obtained in this manner have been divided into five arbitrary categories (Fig. 2): type 1, supraoptimal; 2, ideal; 3, partial; 4, absent; and 5, inverse compensation. Figure 2b illustrates type 3 where, although compensation occurs, the original (adapted) level of response is only partially restored (partial compensation).

By analogy, the swimming performance surface of Fig. 1 lends itself to description in terms of capacity adaptation. Over much of that surface, compensation appears to be inverse (type 5). For example, the swimming rate of a coho juvenile acclimated to t_1 (e.g. 10 C) is about 4.5 lengths/s (L/s). Performance of the fish, raised to t_2 (e.g. 20 C) and measured acutely, would be about 5.5 L/s. After the fish is acclimated to t_2, its swimming rate should rise further to about 5.8 L/s.

Resistance adaptations may be demonstrated on pairs of warm-adapted and cold-adapted rate curves by extending acute measures of response to temperatures outside the normal range ("ex-

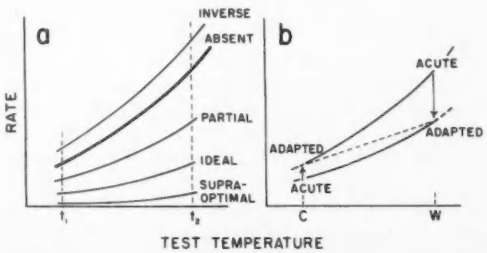

FIG. 2. Types of capacity adaptation (rate compensation). a, Rate curves are shown for two temperatures (t_1, t_2) in the "normal range" for an organism adapted to t_1, raised acutely to t_2 (heavy line), allowed to acclimate to t_2, then returned acutely to t_1 (lighter lines); b, The course of partial compensation, as an example, shows rate changes for cold-adapted (C) or warm-adapted (W) organisms moved to the second temperature; the broken line shows the relation between the adapted rates at the two temperatures (modified in part from Precht 1961).

tremes"). The stylized rate curves of Fig. 3, assembled by Precht from numerous studies of living material, frequently have been used to illustrate two types of resistance adaptations. *Reasonable adaptations* are those where heat resistance increases and cold resistance decreases with increase in adaptation temperature (e.g. Fig. 1). *Paradoxical adaptations* are those where heat resistance decreases and cold resistance increases with increase in adaptation temperature.

Finally, it should be pointed out that response surface configuration implied from these concepts is that defined over short intervals of time. Such relatively "fixed" responses are equivalent to Precht's *unchanging reaction* systems. Over extended periods of time, however, surface configuration may change with growth or season (Griffiths and Alderdice 1972; Alderdice 1972), as may the incipient lethal boundaries (Tyler 1966); these changes are equivalent to variations occurring under Precht's *changing reaction systems*. The distinction will not be developed further, but is made to complete the general argument. By analogy, changing reaction systems could be represented by a strip of motion picture film illustrating dynamic properties of a surface in time; the surface shown in Fig. 1 would then represent a single frame.

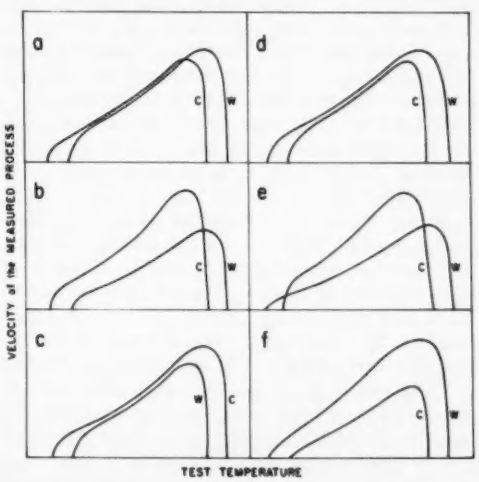

FIG. 3. Schematic representation of the influence of acute (test) temperatures on rate processes of various cold-adapted (C) and warm-adapted (W) organisms: a, reasonable cold and heat adaptation, compensation absent; b, reasonable cold and heat adaptation with compensation; c, reasonable cold and paradoxical heat adaptation, compensation absent; d, paradoxical cold and reasonable heat adaptation, compensation absent; e, paradoxical cold and reasonable heat adaptation, partial compensation; f, paradoxical cold and reasonable heat adaptation, inverse compensation (adapted from Precht 1959, 1967).

Synthesis

The rate–temperature curves that have been presented are, of course, selected transects (warm-, cold-acclimated) of rate surfaces whose axes are acclimation (adaptation) and acute (test) temperature (e.g. Fig. 1). For example, the pair of rate curves from Fig. 3a are reproduced in Fig. 4 (lower panel) as transects of a rate surface (upper panel) at two arbitrary levels (w, warm; c, cold) of acclimation temperature. Isopleths of rate on the surface have been added (upper panel) on the basis of the arbitrary scale in the lower panel.

In this manner types of rate surfaces may be constructed (Fig. 5) that satisfy the characteristics of each pair of rate curves of Fig. 3. Note

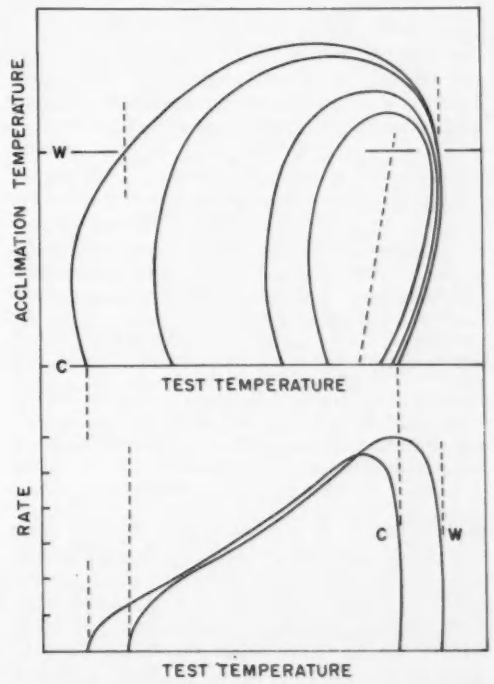

FIG. 4. Rate surface (*upper*) constructed from the pair of rate–temperature curves (*lower*) from Fig. 2a. Placement of the cold-adapted (C) and warm-adapted (W) curves, as transects of the upper panel, is arbitrary. Isopleths of rate (*upper*) have been drawn freehand through loci of equal rate on the two lower (C, W) transects. The diagonal broken line (*upper*) joins the test temperatures of maximum rate from the two lower (C, W) curves.

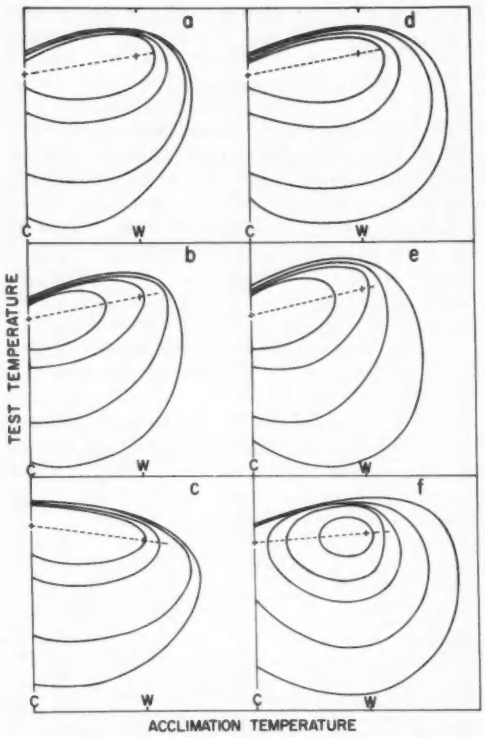

FIG. 5. Schematic rate surfaces, constructed as in Fig. 4, based on the cold-adapted (C) and warm-adapted (W) rate curves of Fig. 2 considered as surface transects. The major axes of the surfaces are approximated by the broken lines through the center region of each surface. These axes join the "turning points" (Umkehrpunkte) of the Precht rate curves. On these axes, assumed analogous to the test-temperature axis of Fig. 1, would be found the test (acute) temperatures associated with maximum rate (crosses) for each acclimation temperature.

that in Fig. 5 the temperature scales have been transposed; rate surfaces based on Precht's models may then be considered relative to Fry's thermal tolerance polygon. The reader is cautioned, however, against extensive interpretation of these stylized surfaces. The main reason for showing them is to illustrate some of their suggested properties, in the hope of generating further enquiry. It would be appropriate at this point to illustrate capacity surfaces in terms of metabolic rate. However, for reasons outlined earlier, little complete evidence of this nature is available (Fry and Hochachka 1970, p. 102–103).

A tentative analogy may now be presented, relating the Fry and Precht concepts of adaptation. Precht's "rate curves," describing either metabolic rates or levels of activity, may be considered as transects across a rate surface bounded by a Fry temperature tolerance polygon. Therefore, changes in metabolic rate or active capacity, within the tolerance polygon, will approximate capacity changes within Precht's normal range of temperatures. Changes in those levels, beyond the zone of tolerance, will approximate *capacity* changes at Precht's temperature extremes. That is, Precht's *resistance adaptations* are analogous to changes in *capacity* occurring in the zone of resistance of Fry.

Discussion

Implicit in the following discussion is the assumption that preexperimental temperature history is known. The boundaries of the zone of tolerance, and effective times at temperatures beyond the incipient lethal level, are a function of the temperature of prior acclimation, other factors contributing to the acclimation state being equal (e.g. size, season, oxygen supply). Measures of capacity within the zone of tolerance also are dependent on the time course of metabolic adjustment after a preparation is shifted to a new, acute temperature. The influence of other activities and their associated compartments of metabolism may also modify the measured rates. Meaningful measurements under these circumstances may require a better appreciation of the nature and time course of thermal acclimation, and appreciation of the potential biases imbedded in a measure of response resulting from other compartments of metabolic demand.

In this regard a fundamental difference occurs in the methods used by the two schools of thermal adaptation. Fry employs sudden transfers of fish from acclimation to constant, acute temperatures, and determines incipient lethal levels approximately as the asymptote of a distribution of effective times. Precht (Christophersen and Precht 1952; Precht et al. 1966) and many other investigators often employ steadily increasing or decreasing temperatures, starting at the acclimation level and measuring response rates at various temperatures throughout the course of temperature change. In general, the latter is the method for obtaining the *critical thermal maximum* (CTM). This technique tends to confound time and temperature; it tends to raise or lower the upper and lower lethal temperatures, respectively (Fry 1971). Although the process is not at all well understood, it appears the lethal temperature will depend on the rate of temperature change, which influences both the time available for acclimation and the time of exposure to temperatures at and

beyond the incipient lethal level (Cocking 1959). Hence, use of the CTM can lead to differences in acutely determined measures of capacity and determinations of lethal temperature, depending on the rate of temperature change employed.

With these qualifications in mind and with reservations arising from the paucity of real data, the attributes of temperature adjustment so far considered will be discussed further in relation to the rate surface of Fig. 1.

Capacity Adaptations

In general, changes in metabolic rate or active capacity, measured acutely for given acclimation temperatures within the "normal" range, generate surfaces whose contours reflect both acclimation and acute temperature experience. Conversely, from such a surface the relation of rates on any pair of transects may be estimated. On the surface a parallelogram may be constructed, starting at the equal temperature diagonal (e.g. Fig. 1), to show: the acclimated rate at temperature t_1, the acute rate after transfer to t_2, the acclimated rate after adjustment to t_2, the acute rate after return to t_1, and the final rate when acclimation to t_1 is again complete.

The "turning point" of these curves (temperature at which the maximum rate occurs on a transect) may or may not be found within the zone of tolerance, depending on the biological material examined and the response measured. For swimming speeds of intact fish (Fig. 1), the turning point occurs within the zone of tolerance and is found on the "test-temperature axis." Furthermore, the test-temperature axis of maximum capacity and the upper incipient lethal boundary are approximately parallel, suggesting that the former may provide information on the slope although not the exact location of the latter (cf. Fig. 1, 5). In general, it is assumed that the temperature ridge of maximum capacity occurs near or beyond the upper boundary of the zone of tolerance. In addition, some cellular preparations may show changes in capacity at Precht's "normal" temperatures, but show little or no resistance adaptation (see Berkholz 1966; his fig. 4). Hence, the temperature of maximum capacity may be constant at increasing acclimation temperatures. That is, maximum rates in some instances may be found on the equivalent test-temperature ridge of Fig. 1, and the ridge would parallel the acclimation temperature axis.

Finally, there is one major point to be made regarding the five compensation types defined under Precht's capacity adaptation. Determination of compensation type can depend on the nature of the capacity surface and the choice of temperatures in the standard two-temperature comparison. This can be demonstrated by erecting a two-temperature parallelogram on any of the surfaces illustrated (Fig. 1, 5) in the manner described earlier. Although those on the swimming speed surface of Fig. 1 will resemble inverse compensation, it can be shown that compensation type, in general, will depend on 1) the slope of the major (test-temperature) axis of the capacity surface relative to the acclimation temperature axis, 2) the occurrence and location of a temperature locus of ultimate maximum capacity within or beyond the boundary of the tolerance polygon, and 3) the two temperatures (transects) selected in the comparison. Further understanding of the nature of the capacity surface would require investigation of, perhaps, five surface transects, rather than the two generally made.

Transition Between Capacity and Resistance

The limits of a capacity surface, for intact organisms, are conveniently defined by the incipient lethal boundaries. For suborganismic preparations the analogous boundaries have not been defined. Much work has been done on enzyme activity and metabolic rate of cell preparations; in general, however, the techniques employed confound time and temperature in the determination of metabolic rate or extent of enzyme deactivation (e.g. by using a constant short exposure time at a series of acute temperatures).

One possible approach would be the determination of resistance (exposure) time (to 50% mortality or an equivalent metameter) at a series of acute temperatures, with possible correction for control mortality using the acclimation temperature as a control. A number of such determinations on preparations from various acclimation temperatures should produce a family of truncated rectangular hyperbolae. These would be equivalent to Fry's (untransformed) resistance lines (e.g. Fry 1947; his fig. 5). The exposure time asymptote of each distribution should approximate the incipient lethal temperature for each acclimation temperature investigated. The series of asymptotes obtained should define the incipient lethal boundary.

Further estimates could be investigated, in the same manner, using the temperature at the point of intersection of the two limbs of an Arrhenius plot of selected measures of metabolic rate or active capacity.

Resistance Adaptations

With the setting of incipient lethal boundaries

on Precht rate curves, resistance adaptations would be equivalent to measures of change in capacity in the zone of resistance of Fry. Basically, resistance adaptations as measured are comparable to the changes in swimming performance shown in Fig. 1 when performance is measured acutely outside of the zone of tolerance. Where upper lethal boundaries have not been determined, it is assumed that investigation would occur on transects of the surface at and beyond the test-temperature axis of maximum capacity. In this respect it is noted that the slope of the test-temperature axis, relative to the acclimation axis, may suggest the form of the upper incipient lethal boundary. However, the lack of parallelism between swimming speed isopleths and the lower incipient lethal boundary in Fig. 1 suggests that a similar association does not occur at low lethal temperatures.

Precht's definitions of reasonable and paradoxial resistance adaptations are based on comparisons involving shifts in the course, magnitude, and turning points of cold-adapted and warm-adapted rate curves. Examination of the incipient lethal boundaries in Fig. 1 suggests that rate surfaces and their lethal boundaries can lead to similar interpretations. The example (Fig. 1) is one of reasonable heat adaptation and reasonable cold adaptation. That is, increase in acclimation temperature leads to decrease in cold tolerance and increase in heat tolerance. Undoubtedly, the same conclusion would be reached by comparing a number of transects of the swimming speed *capacity* surface shown in the figure, as the test-temperature axis of maximum swimming capacity and the upper incipient lethal temperature boundary are approximately parallel. In contrast, and by similar argument, paradoxical resistance adaptation would suggest that the upper incipient lethal temperature boundary would parallel the turning-point axis (e.g. Fig. 5c); that is, both capacity and tolerance probably decrease together at higher acclimation temperature levels.

ALDERDICE, D. F. 1972. Factor combinations, p. 1659–1722. *In* O. Kinne [ed.] Marine ecology. Vol. 1. Environmental factors, Part 3. Wiley-Interscience, London.

BERKHOLZ, G. 1966. Über die Temperaturadaptation des Nerflings (*Idus idus*, Pisces) nach inkonstanter Vorbehandlung. Z. Wiss. Zool., Abt. A. 174: 377–399.

BRETT, J. R. 1952. Temperature tolerance in young Pacific salmon, genus *Oncorhynchus*. J. Fish. Res. Board Can. 9: 265–323.

CHRISTOPHERSEN, J. 1967. Adaptive temperature responses of microorganisms, p. 327–348. *In* C. L. Prosser [ed.] Molecular mechanisms of temperature adaptation. Publ. 84, Am. Assoc. Adv. Sci., Washington, D.C. Horn-Shafer Co., Baltimore, Md.

CHRISTOPHERSEN, J., AND H. PRECHT. 1952. Untersuchungen zum Problem der Hitzeresistenz. I. Versuche an Karauschen (*Carassius vulgaris* Nils). Biol. Zentralbl. 71: 313–326.

1953. Die Bedeutung des Wassergehaltes der Zelle für Temperaturanpassungen. Biol. Zentralbl. 72: 104–119.

COCKING, A. W. 1959. The effects of high temperature on roach (*Rutilus rutilus*). II. The effects of temperature increasing at a known constant rate. J. Exp. Biol. 36: 217–226.

FRY, F. E. J. 1947. Effects of the environment on animal activity. Univ. Toronto Stud. Biol. Ser. 55, Publ. Ont. Fish. Res. Lab. 68: 1–62.

1971. The effect of environmental factors on the physiology of fish, p. 1–98. *In* W. S. Hoar and D. J. Randall [ed.] Fish physiology. Vol. 6. Environmental relations and behaviour. Academic Press, Inc., New York and London.

FRY, F. E. J., J. R. BRETT, AND G. H. CLAWSON. 1942. Lethal limits of temperature for young goldfish. Rev. Can. Biol. 1: 50–56.

FRY, F. E. J., AND P. W. HOCHACHKA. 1970 Fish, p. 79–134. *In* G. C. Whittow [ed.] Comparative physiology of thermoregulation. Academic Press, Inc., New York and London.

GRAINGER, J. N. R. 1958. First stages in the adaptation of poikilotherms to temperature change, p. 79–91. *In* C. L. Prosser [ed.] Physiological adaptations. Ronald Press, New York, N.Y.

1960. The early phases in the adjustment of respiratory rates of unicellular organisms to new temperatures and the simulation of these in a model. Z. Wiss. Zool., Abt. A. 163: 317–341.

GRIFFITHS, J. S., AND D. F. ALDERDICE. 1972. Effects of acclimation and acute temperature experience on the swimming speed of juvenile coho salmon. J. Fish. Res. Board Can. 29: 251–264.

PETERSEN, R. H., AND J. M. ANDERSON. 1969. Influence of temperature change on spontaneous locomotor activity and oxygen consumption of Atlantic salmon, *Salmo salar*, acclimated to two temperatures. J. Fish. Res. Board Can. 26: 93–109.

PRECHT, H. 1949. Über die Temperaturabhängigkeit von Lebensprozessen. Z. Naturforsch. 46: 26–35.

1958. Concepts of temperature adaptation of unchanging reaction systems of cold-blooded animals, p. 50–78. *In* C. L. Prosser [ed.] Physiological adaptations. Ronald Press, New York, N.Y.

1959. Untersuchungen über die Resistenzadaptation einiger Organfunktionen von Warmwasserfischen gegenüber extremen Temperaturen. Z. Vgl. Physiol. 42: 365–382.

1961. Temperaturanpassungen bei wechselwarmen Tieren. Zool. Anzeiger 24: 38–60.

1964. Über die Resistanzadaptation wechselwarmer Tiere an extreme Temperaturen und ihre Ursachen. Helgol. Wiss. Meeresunters. 9: 392–411.

1967. A survey of experiments on resistance adaptation. p. 307–321. *In* A. S. Troshin [ed.] The cell and environmental temperature. Pergamon Press, Oxford.

1968. Der Einfluss "normaler" Temperaturen auf Lebensprozessen bei wechselwarmen Tieren unter

Ausschluss der Wachstums- und Entwicklungsprozesse. Helgol. Wiss. Meeresunters. 18: 487–548.

PRECHT, H., T. BASELOW, R. BERECK, F. LANGE, W. THIEDE, AND L. WILKE. 1966. Reaktionen und Adaptationen wechselwarmer Tiere nach einer Änderung der Anpassungstemperatur und der zeitliche Verlauf. Helgol. Wiss. Meeresunters. 13: 369–401.

PROSSER, C. L. 1958. General summary: the nature of physiological adaptation, p. 167–180. *In* C. L. Prosser [ed.] Physiological adaptation. Ronald Press, New York, N.Y.

TROSHIN, A. [ed.] 1967. The cell and environmental temperature. Pergamon Press, Oxford. x + 462 p.

TYLER, A. V. 1966. Some lethal temperature relations of two minnows of the genus *Chrosomus*. Can. J. Zool. 44: 349–364.

Scope for Metabolism and Growth of Sockeye Salmon, *Oncorhynchus nerka*, and Some Related Energetics[1]

J. R. BRETT

Department of the Environment, Fisheries and Marine Service, Pacific Biological Station, Nanaimo, B.C. V9R 5K6

BRETT, J. R. 1976. Scope for metabolism and growth of sockeye salmon, *Oncorhynchus nerka*, and some related energetics. J. Fish. Res. Board Can. 33: 307–313.

The extent of metabolic and feeding requirements for fingerling sockeye salmon (*Oncorhynchus nerka*) are compared over the tolerable range of temperature. Scope for growth, derived from the difference between maximum and maintenance rations, is shown to relate to temperature in a manner similar to that for maximum growth rate. Metabolic scope is compared with scope for growth, supporting the general concept of scope for activity developed by Fry (1947).

BRETT, J. R. 1976. Scope for metabolism and growth of sockeye salmon, *Oncorhynchus nerka*, and some related energetics. J. Fish. Res. Board Can. 33: 307–313.

L'auteur compare les exigences métaboliques avec celles de l'alimentation chez des alevins de la grosseur du doigt de saumon nerka (*Oncorhynchus nerka*) dans l'intervalle tolérable de température. Il démontre que la sphère de croissance, dérivée de la différence entre les rations maximales et de subsistance, est liée à la température de la même façon que celle du rythme de croissance maximal. Il compare la sphère du métabolisme avec celle de la croissance, appuyant le concept général de sphère d'activité développé par Fry (1947).

Accepted October 28, 1975 Accepté le 28 octobre 1975

THE concept of *scope for activity* was first elaborated by Fry (1947) as the difference between active and standard metabolic rates. This "metabolic scope" defined the amount of energy available for activity, over the tolerable range of temperature. Fry (1947, 1971) demonstrated that the maximum sustained swimming speed of fish was closely correlated with metabolic scope and not active metabolic rate, a relation that is particularly apparent at high temperatures. Although touching on a broad range of activities requiring energy expenditure (e.g. rates of locomotion, fecundity, branchial ventilation, development, heartbeat — for various organisms) by far the greatest attention was devoted to levels of locomotion in fish, either as spontaneous activity or as imposed swimming speeds. These were studied in relation to rates of oxygen consumption and the effects of environmental factors. Fry (1971) stated that he was essentially concerned with catabolism — "the sum of the reactions which yield the energy the organism utilizes." Growth, an anabolic process, was recognized as an activity, and used in one illustration to show the limiting effects of fluctuating levels of oxygen (Whitworth 1968, quoted by Fry 1971).

Warren and Davis (1967) paid tribute to Fry's concept of *scope for activity* and elaborated a

[1]This paper forms part of the proceedings of a symposium convened at the Harkness Laboratory of Fisheries Research, October 1974, in honor of Professor F. E. J. Fry, M.B.E., M.A., Ph.D., D.Sc., F.R.S.C.

Printed in Canada (J4031)
Imprimé au Canada (J4031)

scope for growth, which they tentatively considered to be "the difference between the energy of the food an animal consumes and all other energy utilizations and losses." These authors recognized that the anabolic aspects of food consumption cannot be considered in the same context with the catabolic relations of active and standard metabolic rates, although one system obviously influences the other. A number of examples of scope for growth depicted as growth rates in relation to temperature were given by Warren and Davis (1967) in conjunction with certain associated bioenergetic relations, namely: food consumed, fecal wastes, specific dynamic action, and starving metabolic rate. However, these do not by themselves involve a calculated scope (by difference) such as Fry applied to metabolic rates.

It was also noted by Fry (1947) that environmental factors operate through metabolism to affect activity, and not directly on the activity itself. Similarly, environmental factors will not act directly on growth; the pathway will be through the mechanisms of energy supply and demand influencing the scope, in a way that Warren and Davis (1967) implied but did not actually determine. Warren (1971) further elaborated on this thesis, illustrating the theoretical effects of limiting food on the energy budget and the deduced scope for growth.

It is apparent that a clear distinction must be made between the activity itself (growing, excreting, contracting, respiring, etc.) and the source of available energy providing for that activity. The source is presumably a measurable metabolic component of the food intake; in the case of growth it would be an anabolic component.

As a result of research on both the metabolic rates and the feeding rates of young sockeye salmon in relation to the respective activities of swimming (Brett 1964) and growing (Brett et al. 1969), a revealing comparison of the energy relations involved in the two scopes can be made. The terminology of Fry (1957) will be used for metabolic rates, with indicated abbreviations, and that adopted by Brett et al. (1969) used for growth relations; standard metabolic rate (S_{met}), active metabolic rate (A_{met}), maximum growth rate (G_{max}), maximum ration (R_{max}), maintenance ration (R_{maint}).

Energy Costs

Energy Conversions

The common unit of rate of energy exchange for metabolism and growth has been chosen as kcal/kg per h. Metabolic rates have been converted by applying an oxycalorific equivalent of 3.36 cal/mg O_2 or 4.8 kcal/liter O_2. Brafield and Solomon (1972) have shown that if protein metabolism is the main source of energy and ammonia the main excretory product, a value of 3.20 cal/mg O_2 is applicable. However, for sustained performance of sockeye salmon it was demonstrated that lipids (3.30 cal/mg O_2) may contribute over half the energy; in addition some carbohydrate (3.53 cal/mg O_2) utilization is involved (Brett 1973). Further it has been observed that the respiratory quotient (RQ) of fish is frequently over 0.8 during periods of excitement indicating some carbohydrate metabolism (Kutty 1968, 1972). Hence the value of 3.36 cal/mg O_2 was selected; it differs by only 5% from the protein-based value of Brafield and Solomon (1972).

The caloric food values involved are those recorded in Brett et al. (1969). The mean value was 5.45 kcal/g of dry food. In the experiments described in 1969, fish were fed a measured amount in terms of dry food calculated as a percent of the dry body weight, which was then converted back to the equivalent amount per kg of wet weight. The moisture content of a 30-g fish on maintenance ration is about 78%. A ration of 1%/day is equivalent to 2.2 g dry food/kg of fish (wet) per day or approximately 0.50 kcal/kg per h. Sockeye fingerlings on a maximum ration have a moisture content of about 72% (Brett et al. 1969). Since there is more dry weight per kg of wet weight of fish, a ration of 1%/day is equivalent to 0.64 kcal/kg per h.

These values represent the total caloric energy in the food. Because of a nondigestable fraction and an excreted fraction, a physiological value of 80% of the total energy has frequently been used for assessing the net energy (e.g. Winberg 1956, Paloheimo and Dickie 1966). While there is justification for this fraction when the diet is virtually devoid of carbohydrate, as in most natural foods, artificial foods are formulated with some cheap carbohydrate to economize on the use of protein as an energy source. The digestibility of carbohydrate (e.g. raw cereal starches) has been studied for trout by Phillips and associates (Phillips 1969; Phillips and Brockway 1959). Using Phillips' (1969) physiological values,[2] only 72% of the energy is available for use, providing 3.92 kcal/g dry food. A unit value of 1% dry wt/kg per day therefore equates to

[2]Kilocalories per gram for protein = 3.9, fat = 8.0, and carbohydrate = 1.6. More digestible carbohydrate is incorporated in present diets (Halver 1972).

0.36 kcal/kg per h for maintenance ration and 0.46 kcal/kg per h for maximum daily ration.

Size Considerations

The size and age of sockeye studied in the two cases (metabolic rates, growth rates) were not identical. Both were yearling fish, ranging in weight from either 33 to 66 g with a mean of 48 g (metabolism), or 6 to 29 g with a mean of 13 g (growth). Correction of metabolic rates for comparing similar weights of sockeye has been shown to follow a weight exponent of 0.88 for standard metabolism and 0.99 for active metabolism (Brett and Glass 1973). For the difference in mean weights of the two groups this would involve at most a 10% correction (S_{met}), ranging to less than 1% (A_{met}). Weight corrections for size effect on food consumption rates are known from hatchery practices for maximum rations (Haskell 1959) but not for maintenance rations. Since growth rate falls more rapidly than metabolic rate with increasing size, a greater correction than 0.88 is undoubtedly involved. However, by considering the following analysis to apply to sockeye weighing an average of 30 g, only a small error for weight correction (±18 g) could enter into the comparisons; the emphasis is on the principles involved.

Maintenance Levels

Studies of the "maintenance cost" or "maintenance requirement" of domestic animals, in either a fasting state or steady energetic state (no weight change), are frequently conducted to establish minimum energy expenditure under different environmental conditions and diets (Brody 1945; Kleiber 1961; Blaxter 1965). Direct calorimetry (heat production) and indirect calorimetry (oxygen consumption) are used in the case of the fasting animal to obtain the basal or standard metabolic rate. Minimum feeding rates that just maintain the animal without any growth define the maintenance requirement for a particular feed formulation. Under energetically demanding environmental conditions (e.g. extremes of temperature) the cost of maintenance can be high, amounting to half the active metabolic rate in some fishes. These respective energetic costs for fish were reviewed by Fry (1957) in regard to standard metabolic rates, and by Brown (1957) for maintenance feeding requirements.

Since feeding, even at the maintenance level, invokes activity two intermediate levels of metabolism are considered: 1) routine metabolic rate (R_{met}), that rate generated by spontaneous activity in otherwise unstimulated fish, and 2) feeding metabolic rate (F_{met}). Data for routine metabolic rates of sockeye are recorded in Brett (1964). Those for feeding metabolic rates have been drawn from a series of experiments in which the total daily oxygen consumption was recorded for yearling sockeye, on different planes of nutrition, above and below the maintenance level. (A small portion of this unpublished work was presented in Brett (1970).)

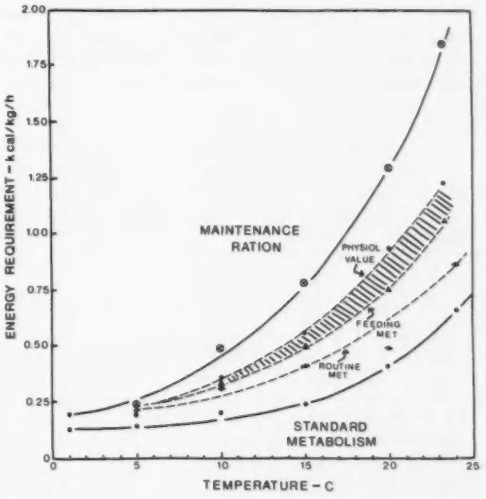

FIG. 1. Energy requirement of yearling sockeye salmon (*Oncorhynchus nerka*) for standard metabolism and maintenance ration, over the tolerable range of temperature. The metabolic rate associated with feeding at the maintenance level (F_{met}) is shown together with the amount normally expended in spontaneous activity (routine metabolism). The net energy available from the maintenance ration is shown as the physiological value. The shaded area is unaccounted energy, probably attributable to an increasing inefficiency of food conversion, i.e. a reduced physiological value at higher temperatures.

The relation that each of these metabolic and feeding requirements bears to temperature is illustrated in Fig. 1. It can be seen that the energy of standard metabolism amounts to approximately two thirds of the maintenance requirement at 1 C, falling to one third at 23 C (Table 1). The two curves can be closely approximated by the equations:

$$\text{Log } (Y - 0.12) = -1.99 + 0.025X \; (S_{met}),*$$

and

$$\text{Log } Y = -0.77 + 0.044X \; (R_{maint}),$$

*Equation from Brett (1964) converted to read in kcal/kg per h.

TABLE 1. Energetic cost of metabolic rates and maintenance rations of yearling sockeye salmon (*Oncorhynchus nerka*) (30 ± 18-g range) in relation to temperature. Equivalents applied: 1 mg O_2/h = 3.36 cal/h; ration of 1%/day = 0.50 kcal/h; physiological value = 0.72 of caloric content.

	Standard met. rate		Routine met. rate[a]		Feeding met. rate		Maint. ration		
							Amt.	Equiv.	Physiol. value
Temp. (C)	(mg O_2/kg per h)	(kcal/kg per h)	(mg O_2/kg per h)	(kcal/kg per h)	(mg O_2/kg per h)	(kcal/kg per h)	(% dry wt per day)	(kcal/kg per h)	(kcal/kg per h)
1	39[b]	0.131	—	—	—	—	0.40	0.20	0.144
5	41	0.138	69	0.232	73[c]	0.246	0.48	0.24	0.173
10	60	0.201	99	0.333	100	0.336	0.98	0.49	0.352
15	71	0.238	124	0.417	145	0.487	1.56	0.78	0.562
20	120	0.403	160	0.538	225	0.753	2.60	1.30	0.936
24	196	0.658	251	0.842	315[c]	1.06	3.7[d]	1.85	1.22

[a]Average value from Tables I and III in Brett (1964).
[b]Determined from equation in Brett (1964).
[c]Extrapolated value.
[d]Temp = 23.3 C.

where Y is rate of energy exchange (kilocalories per kilogram per hour) and X is temperature (C).

Because of the higher level of energy cost associated with high temperatures, the relative accuracy of the determination is technically greater at 23 C than 5 C. The greater slope of R_{maint} than S_{met} indicates an increasing cost of food processing with rising temperature. This is partly attributable to an increasing cost of F_{met}. While F_{met} accounts for 93% of R_{maint} at 5 C, the proportion is approximately 57% at 23 C. The unaccounted energy balance at all temperatures is most likely made up of energy-containing, nitrogeneous excretory products and discharged fecal losses. Normal nitrogenous wastes in the form of ammonia and urea would account for 14.5% of the protein consumed (Krueger et al. 1968), i.e. 14.5% of 62%,** which equals 9% of the total food energy. This leaves one third of R_{maint} above 15 C to be accounted for through feces and excessive nitrogenous excretion. The physiological value of the food does not account for all of this, as indicated in the shaded area of Fig. 1. This could be ascribed to SDA, the heat loss during digestion; however, proof is not available. Indeed, this is considered to be included in F_{met} as recorded. From the great inefficiency of food processing by this species at temperatures above 20 C (Brett et al. 1969), it is likely that the physiological value becomes progressively in error as temperature increases above the optimum for growth.

MAXIMUM LEVELS

The active metabolic rate of sockeye rises exponentially with increasing temperature up to 15 C where it levels off, decreasing slightly at higher temperatures (Fig. 2, Table 2). This sharp discontinuity in the curve appears to be the result of limiting oxygen in air-saturated fresh water, above 15 C (Brett 1964, and further discussed by Fry 1971). Whatever the reason it contrasts with the shape of the curve for maximum food intake (R_{max}) which rises in a concave sweep

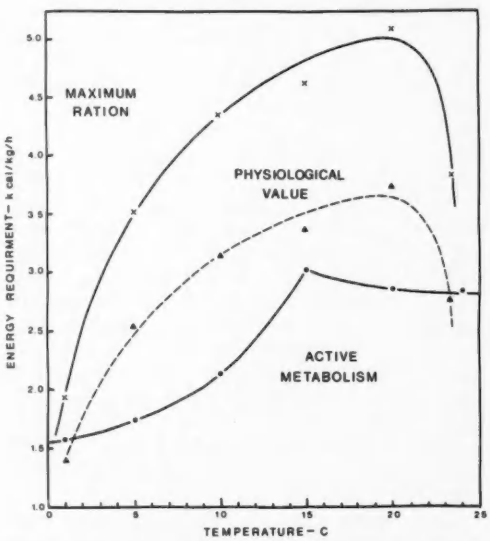

FIG. 2. Energy requirement of yearling sockeye for active metabolic rate compared with the energy intake of maximum ration, in relation to temperature. Physiological food values indicate net energy available.

**Protein energy = 62% of total in ration.

TABLE 2. Energetic cost of active metabolic rate and daily maximum food intake of yearling sockeye salmon in relation to temperature.

	Active met. rate		Maximum ration		
			Amt.	Equiv.	Physiol. value
Temp. (C)	(*mg O_2/kg per h*)	(*kcal/kg per h*)	(*% dry wt/ day*)	(*kcal/kg per h*)	(*kcal/kg per h*)
1	470[a]	1.58	3.0	1.92	1.38
5	514	1.74	5.5	3.52	2.53
10	627	2.11	6.8	4.35	3.13
15	895	3.01	7.2	4.61	3.32
20	852	2.86	8.1	5.18	3.73
24	848	2.85	6.0[b]	3.84	2.76

[a]Determined by extrapolation.
[b]Temp = 23.3 C; value very sensitive to temperature, with wide variance.

to 20 C and then inflects steeply downward as appetite and conversion efficiency fall off near the upper lethal temperature.

For this size of sockeye the physiological value of the food (R_{max}) still provides enough net energy to meet the full demand of active metabolism, except at the extreme limits of temperature tolerance (Fig. 2). However, as stated, with increasing size the intake falls such that larger fish (over 50 g at most) would not consume enough to meet the energy requirements of active metabolism. This presumes that fish forced to maintain such an unusually high metabolic rate would not compensate by significantly increased food intake over the maximum measured to date.

Energy Available

Scope for Activity

The metabolic scope for activity is shown in Fig. 3 in relation to the respective active and standard metabolic rates and the maximum sustained swimming speed. The effect of an increasing standard metabolic rate at high temperatures coupled with no increase in active metabolism results in a pronounced decline in scope above 15 C. This is reflected in a parallel decline in sustained swimming speed. The maximum continuous rate at which energy can be made available for locomotion is approximately 2.75 kcal/kg per h. For the mean length of the sockeye tested (18.8 cm) the speed attained was 77.4 cm/s or 4.12 lengths/s (Brett 1964).

Scope for Growth

A similar compilation of the feeding rate–growth relations is also presented in Fig. 3 for comparison within and between the two energetic systems. The similarity of shape between the growth scope and growth rate curves is apparent, supporting the derivation of growth scope from measures of R_{max}–R_{maint}. The maximum available energy for growth is estimated to be 2.9 kcal/kg per h at 15 C. The precipitous drop in scope above 20 C is reflected in a parallel decline in growth rate, despite a food intake of approximately 2.5 kcal/kg per h at 23 C.

It is apparent that the metabolic scope for activity could not be used to predict the growth rate × temperature relations with any degree of accuracy. As was suggested in the introduction a catabolic expression cannot be expected to apply directly to an anabolic process. In this sense "scope for activity" does have some limitations in regard to the type of activity considered. Hence "metabolic scope" has been used in Fig. 3 as a more appropriate term. More precisely it might be better to use "catabolic scope" and " anabolic scope"; however, this consideration is not meant to burden the concepts with additional terminology but rather to make a distinction which should lead to greater clarity of understanding.

It is concluded that a simple means for determining growth scope is afforded from ration measurements, and that the general scope for activity concept is supported in the fashion that Fry first elaborated in 1947.

If this is indeed true, then the application of a *limiting factor* (reduced food availability) to the scope for growth should predict the consequent pattern of growth in relation to temperature, a *controlling factor*. In Fig. 3 two hypothetical levels of restricted ration have been applied to the feeding rate, and the resulting scope for growth determined; this, in turn, is compared with the observed growth relations published by Brett et al. 1969. It is quite apparent that the

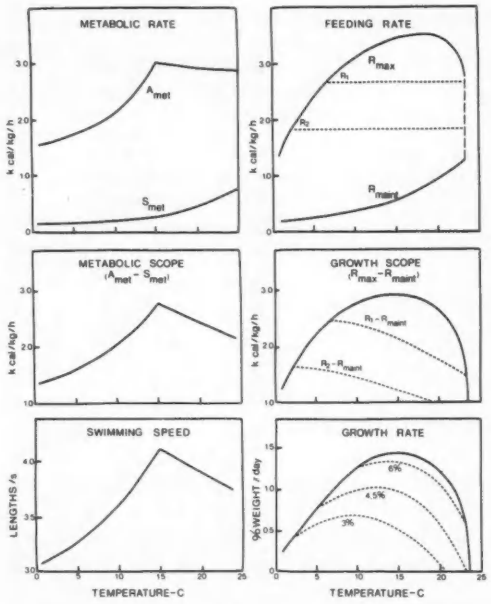

FIG. 3. Comparison of the metabolic and feeding rates used to derive the respective scopes for activity with their corresponding swimming and growth rates. Physiological values have been used for determining the net energy available from food.

Two hypothetical levels of restricted ration (R_1, R_2 — dotted lines) have been applied to the feeding rate. The growth scope is reduced in the manner indicated. For comparison, the observed growth rates of fingerling sockeye are shown in relation to various levels of restricted ration (Brett et al. 1969).

model does have predictive value, particularly in picking up the shift in optimum temperature for growth with decreasing ration (as a consequence of the temperature × ration interaction). This lends further support to the usefulness of the scope concept.

Acknowledgments

Over the years it has been my good fortune to have many stimulating discussions on environmental effects with Dr. F. E. J. Fry. Further associations of value have been with Dr C. E. Warren, and with Dr G. D. Stuffer during his Ph.D. studies (1973) at the University of Washington. These latter studies deal in part with some of the considerations above and should be acknowledged herewith.

BLAXTER, K. L. [ed]. 1965. Energy metabolism. Academic Press, Inc., New York, N.Y. 450 p.

BRAFIELD, A. E., AND D. J. SOLOMON. 1972. Oxy-calorific coefficients for animals respiring nitrogenous substrates. Comp. Biochem. Physiol. 43A: 837–841.

BRETT, J. R. 1964. The respiratory metabolism and swimming performance of young sockeye salmon. J. Fish. Res. Board Can. 21: 1183–1226.

1970. Fish — the energy cost of living, p. 37–52. *In* W. J. McNeil [ed.] Marine aquiculture. Oregon State University Press, Corvallis, Oreg.

1973. Energy expenditure of sockeye salmon, *Oncorhynchus nerka*, during sustained performance. J. Fish. Res. Board Can. 30: 1799–1809.

BRETT, J. R., AND N. R. GLASS. 1973. Metabolic rates and critical swimming speeds of sockeye salmon, *Oncorhynchus nerka*, in relation to size and temperature. J. Fish. Res. Board Can. 30: 379–387.

BRETT, J. R., J. E. SHELBOURN, AND C. T. SHOOP. 1969. Growth rate and body composition of fingerling sockeye salmon, *Oncorhynchus nerka*, in relation to temperature and ration size. J. Fish. Res. Board Can. 26: 2363–2394.

BRODY, S. 1945. Bioenergetics and growth. Reinhold, New York, N.Y. 1023 p.

BROWN, M. E. 1957. Experimental studies of growth, p. 361–400. *In* M. E. Brown [ed.] Physiology of fishes. Vol. 1. Academic Press, Inc., New York, N.Y.

FRY, F. E. J. 1947. Effects of the environment on animal activity. Univ. Toronto Stud. Biol. Ser., 55, Publ. Ont. Fish. Res. Lab. 68: 1–62.

1957. The aquatic respiration of fish, p. 1–63. *In* M. E. Brown [ed.] Physiology of fishes. Vol. 1. Academic Press, Inc., New York, N.Y.

1971. The effect of environmental factors on the physiology of fish, p. 1–98. *In* W. S. Hoar and D. J. Randall [ed.] Fish physiology. Academic Press, Inc., New York and London.

HALVER, J. E. [ed.] 1972. Fish nutrition. Academic Press, Inc., New York and London. 713 p.

HASKELL, D. C. 1959. Trout growth in hatcheries. N.Y. Fish Game J. 6: 204–237.

KLEIBER, M. 1961. The fire of life. An introduction to animal energetics. John Wiley and Sons, Inc., New York, N.Y. 454 p.

KRUEGER, H. M., J. B. SADDLER, G. A. CHAPMAN, I. J. TINSLEY, AND R. R. LOWRY. 1968. Bioenergetics, exercise, and fatty acids of fish. Am. Zool. 8: 119–129.

KUTTY, M. N. 1968. Respiratory quotients in goldfish and rainbow trout. J. Fish Res. Board Can. 25: 1689–1728.

1972. Respiratory quotient and ammonia excretion in *Tilapia mossambica*. Mar. Biol. 16: 126–133.

PALOHEIMO, J. E., AND L. M. DICKIE. 1966. Food and growth of fishes. III. Relations among food, body size and growth efficiency. J. Fish. Res. Board Can. 23: 1209–1248.

PHILLIPS, A. M. JR. 1969. Nutrition, digestion, and energy utilization, p. 351–432. *In* W. S. Hoar and D. J. Randall [ed.] Fish physiology. Vol. 1. Academic Press, Inc., New York and London.

PHILLIPS, A. M. JR., AND D. R. BROCKWAY. 1959. Dietary calories and the production of trout in hatcheries. Prog. Fish Cult. 21: 3–16.

STAUFFER, G. D. 1973. A growth model for salmonids reared in hatchery environments. Ph.D. Thesis. Univ. Washington, Seattle, Wash. 213 p.

WARREN, C. E. 1971. Biology and water pollution control. W. B. Saunders Co., Philadelphia, Pa. 434 p.

WARREN, C. E., AND G. E. DAVIS. 1967. Laboratory studies on the feeding, bioenergetics and growth of fishes, p. 175–214. *In* S. D. Gerking [ed.] The biological basis of freshwater fish production. Blackwell Scientific Publications, Oxford.

WHITWORTH, W. R. 1968. Effects of diurnal fluctuations of dissolved oxygen on the growth of brook trout. J. Fish. Res. Board Can. 25: 579–584.

WINBERG, G. G. 1956. Rate of metabolism and food requirements of fishes. Belorussian State Univ., Minsk. 251 p. (Transl. from Russian by Fish. Res. Board Can. Transl. Ser. No. 194, 1967).

Predation, Yield, and Ecological Efficiency in Aquatic Food Chains[1]

L. M. DICKIE

Department of Oceanography, Dalhousie University, Halifax, N.S.

DICKIE, L. M. 1976. Predation, yield, and ecological efficiency in aquatic food chains. J. Fish. Res. Board Can. 33: 313–316.

Given constancy of biomasses and sizes of predators and prey, the basic ecological equations are used to show that relative predation rates must increase rapidly as trophic level in aquatic food-chains drops towards primary production. The implications of this conclusion for exploitation at different food-chain levels is discussed.

DICKIE, L. M. 1976. Predation, yield, and ecological efficiency in aquatic food chains. J. Fish. Res. Board Can. 33: 313–316.

Supposant que les biomasses et les tailles des prédateurs et des proies sont constantes, nous démontrons à l'aide d'équations écologiques fondamentales que les taux de prédation relatifs doivent augmenter rapidement à mesure que le niveau trophique baisse dans les chaînes alimentaires aquatiques et se rapproche de la production primaire. Nous examinons les implications d'une telle conclusion sur l'exploitation de différents maillons de la chaîne alimentaire.

Accepted October 28, 1975 Accepté le 28 octobre 1975

ECOLOGICAL theory of production systems requires formulation which will permit experimental testing. This is a difficult requirement for any observational science. For aquatic biological systems the uncertainties of successive sampling in situations for which the scales of heterogeneity are so little known make it especially difficult. For this reason it is tempting to try to substitute for observation in time, observations of contrasting stable properties of predator–prey interactions, such as might exist at different levels of the trophic system. The general properties of "food-chains," may now be well enough understood to permit the framing of hypotheses of this type, which could be tested at the level of underlying mechanism. Such tests would be particularly valuable for increasing our confidence in the interpretation of the results of large-scale experiments represented by attempts to manage the exploitation of fisheries resources.

[1]This paper forms part of the proceedings of a Symposium convened at the Harkness Laboratory of Fisheries Research, Algonquin Park, Ontario, October 1974, in honor of Professor F. E. J. Fry, M.B.E., M.A., Ph.D., D.Sc., F.R.S.C.

Printed in Canada (J4032)
Imprimé au Canada (J4032)

Food-Chain Relations

Slobodkin (1972) pointed out that in measuring ecological efficiency we consider relations among three successive levels in a trophic energy flow system. That is, starting with an intermediate trophic level "n," we consider as well, its relations with a predator at a higher trophic level, $n + 1$, and with a prey at a lower level, $n - 1$. Using this terminology, we may define relations among production, biomass and yield, as follows:

$$P_n = K_n I_n$$

and

$$Y_{n+1} = F_{n+1} B_n$$

That is, production (P) of organisms at level n is some function of the efficiency of utilization (K) of their food intake (I), where their food intake $I_n = Y_n$, that is, it is the yield to them from their prey. However, the yield per unit time taken by a predator at trophic level $n + 1$ (Y_{n+1}) is some function (F) of the predation and of the average biomass (B_n) of the prey organisms. The fraction of biomass removed by predation (F_{n+1}) is the instantaneous rate of removal, measured over the interval for which P is measured. It therefore represents the probability of an organism at level n, dying from the action of its predators, and is proportional to some function of predator abundance, activity and grazing efficiency. That is, F_{n+1} is a property of the predator to which the yield accrues, and is identical with instantaneous fishing mortality as it is defined in the fisheries literature (Ricker 1975). We are thus looking at properties involving three successive trophic levels.

With these definitions we may write (Dickie 1972):

$$\frac{Y_{n+1}}{I_n} = F_{n+1} \times \frac{B_n}{P_n} \times K_n \qquad (1)$$

where Y_{n+1}/I_n is the ratio of food intakes at two successive trophic levels. That is, it is a measure of "ecological efficiency" as defined by Slobodkin (1960). From our considerations it is apparent that ecological efficiency can be explicitly defined in terms of three factors: the rate of predation (F_{n+1}), the turnover time or inverse of the specific rate of increase of the biomass ($P_n/B_n = \frac{dB_n}{dt} \times \frac{1}{B_n}$) and the gross production efficiency (K_n), which may be approximated in short-term experiments by the gross growth efficiency.

We may further note that at equilibrium the rate of production and the total rate of mortality (Z_n) of a stock must be the same. If we adopt the conventions of fisheries literature and define the nonpredatory mortality of organisms as M_n, the turnover rate or specific rate of production may be written as:

$$\frac{P_n}{B_n} = (F_{n+1} + M_n) = Z_n$$

These definitions permit us to write, in parallel with the definition of ecological efficiency, two further equations relating the production and biomass in two successive trophic levels:

$$\frac{P_n}{P_{n-1}} = \frac{K_n I_n}{K_{n-1} I_{n-1}} = K_n \times \frac{F_n}{Z_{n-1}} \qquad (2)$$

$$\frac{B_n}{B_{n-1}} = \frac{P_n}{P_{n-1}} \times \frac{Z_{n-1}}{Z_n} \qquad (3)$$

The advantages of writing the relations in this fashion are most readily appreciated by reference to equation (1). That is, ecological efficiency, growth efficiency, and turnover times have all been the subject of special experimental study in aquatic ecosystems. In this form, it appears that the data available may be used to provide information on the less well-known rates of predation (F_{n+1}).

In this particular instance, our principal interest is in the relative predation rates revealed by a comparison of successive trophic levels. Substituting equation (2) in equation (3), we obtain analogous with equation (1):

$$\frac{B_n}{B_{n-1}} = F_n \times \frac{B_n}{P_n} \times K_n$$

Substituting from (1) for the common term B_n/P_n yields the result:

$$\frac{B_n}{B_{n-1}} = \frac{F_n}{F_{n+1}} \times \frac{Y_{n+1}}{I_n} \qquad (4)$$

That is, the ratio of the biomasses of two successive trophic levels of a food chain appears to be same as the ecological efficiency, corrected by the ratio of the predation rates involved. In equation (4) the numerator of the relative predation term is the rate of predation by the "upper" of the two biomasses on the lower, while the denominator represents the rate of predation on the upper trophic level by its own predators.

Interpretations

The clarification of definitions allowed by equation (4) suggests some features of interest in interpreting observations in natural systems.

In the first place, the equation suggests that the ratio of the biomasses of successive trophic levels is independent of the relative average sizes of individuals at these levels, except as they may be reflected in the predation rates. This conclusion was also reached by Kerr (1974) who like Sheldon et al. (1972) based his arguments on similarities in the ratios of sized-related metabolic and growth rates. Kerr did not identify his other independent variables with ecological efficiency. The similarity of his results with that of equation (4) suggests, however, that ecological efficiency is itself a reflection of the ubiquitous metabolic-body size rule, which is emerging as a fundamental "Law of Biology."

Of more particular interest in our immediate discussion is the fact that Kerr's arguments led him to conclude that given a ratio of particle sizes of prey to predator of the order typical among fishes, the ratio of biomasses of predator to prey must be the order of 1:1.2. This is approximately the same as the ratio of biomasses found by Sheldon et al. 1972) to characterize the pelagic zone of the oceans. In terms of equation (4), such observational material on the biomass ratios of trophic levels, together with information on ecological efficiencies, gives us information on the more elusive but practically important relative predation rates.

Slobodkin (1960) appears to have first suggested that ecological efficiencies are probably of the order of 0.10. More recently, however, Steele (1974) has assembled persuasive evidence that in the 3-dimensional statistical–mechanical aquatic world, the more likely value is higher — of the order of 0.20. In the language of equation (4) we thus have the result that $0.8 = \frac{F_n}{F_{n+1}} \times .20$. whence $F_n/F_{n+1} = 4$. That is, as one descends the natural food-chain towards primary production, the rate of predatory exploitation between trophic levels must increase about fourfold for each drop in trophic level.

It has been obvious to planktologists for many years that the degree of utilization of production in the lower food chains must be very high (cf. Platt et al. 1976). Relatively speaking, exploitation rates found among fishes are much lower. However, the suggestion afforded by Sheldon's result that there may be regularity among trophic levels, depending on relative level in the trophic hierarchy, is a surprising and interesting result. If verified, it suggests consequences of significance to both general ecology and fisheries.

In the first place we might reach the conclusion that for each step increase in trophic level in the food chains, we lose approximately 85% of production to decomposers or other "prudent predators" whose feeding does not increase the probability of mortality of the food-organisms (i.e. they were about to die from "other causes"). Conversely, it appears that in the sea a high proportion of substrate for decomposers must first appear in the form of the larger particle sizes.

A second important consequence concerns the effects of artifactual exploitations. With such large predation ratios, reductions of predator abundance, such as happen when an intense fishery sharply reduces the abundance of the large fish-eating sizes of a species, should give rise to a substantial increase in the biomass of the prey. If the top-predator (the fishery) can technologically graze and utilize this prey directly, it would appear that such food-chain shortening should result in substantial increases in the catch per unit effort by the top predator. Such effects may at least partly account for the spectacular growth of pelagic fisheries, such as for herring and capelin, where there have been large increases in the intensity of the traditional demersal fisheries for cod, one of their principal predators.

It is a third consequence, obvious from elementary consideration of size and production relations as well, that under the conditions stated here, a given *amount* of yield from a lower trophic level represents only about 15% of the mortality rate that it would represent at the level of its predator.

Deductions of this sort only make explicit what has tacitly been recognized for many years as the importance that the predator must play in the observed structure of marine food-chains. In the case of fisheries exploitation, however, the consequences they suggest for management of the food-chain structure are very great. One might conclude for example, that far greater emphasis than heretofore should be placed on studies of food-chain linkages and on the technology of capture, than on total fishing intensities and "maximum sustained yield" calculations. The possibility of such effects justifies a considerable effort to test the validity and applicability of the formulation to the interpretation of events in natural systems. Such tests may be possible through study of the logical compared with actual mechanisms operating at the level of individual physiological–behavioral predator–prey links of food-chains in association with productivity or biomass differences.

DICKIE, L. M. 1972. Food chains and fish production, p. 201–221. *In* Environmental conditions in the NW At-

lantic. Int. Comm. Northwest Atl. Fish., Spec. Publ. 8: 254 p.

KERR, S. R. 1974. Theory of size distribution in ecological communities. J. Fish. Res. Board Can. 31: 1859–1862.

PLATT, T., K. DENMAN, AND A. JASSBY. 1976. Modelling primary production. *In* J. H. Steele [ed.] The seas. Vol. 6. Wiley-Interscience Publishers, New York, N.Y. (In press)

RICKER, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191: 382 p.

SHELDON, R. W., A. PRAKASH, AND W. H. SUTCLIFFE JR. 1972. A size distribution of particles in the ocean. Limnol. Oceanogr. 17: 327–340.

SLOBODKIN, L. B. 1960. Ecological energy relationships at the population level. Am. Nat. 94: 213–236.

1972. On the inconstancy of ecological efficiency and the form of ecological theories. Trans. Com. Acad. Arts Sci. 44: 293–305.

STEELE, J. H. 1974. The structure of marine ecosystems. Harvard University Press, Cambridge, Mass. 128 p.

Selective Breeding and Hybridization in Fisheries Management[1,2]

PETER IHSSEN

Fish and Wildlife Research Branch, Ontario Ministry of Natural Resources, Maple, Ont.

IHSSEN, P. 1976. Selective breeding and hybridization in fisheries management. J. Fish. Res. Board Can. 33: 316–321.

Selective breeding of fish using quantitative genetic techniques is discussed. Fish offer advantages over other livestock for selective breeding procedures because of their relatively high reproductive potential and low reproductive barriers.

Maintaining fish stocks in artificial environments can cause undesirable genetic changes such as loss in heterozygosity due to inbreeding and loss in fitness. Methods to minimize inbreeding are given. The study of cross breeds of inbred lines, and hybrids among strains or even species, to produce high levels of heterozygosity and heterosis or hybrid vigor is suggested.

IHSSEN, P. 1976. Selective breeding and hybridization in fisheries management. J. Fish. Res. Board Can. 33: 316–321.

Nous discutons de croisements sélectifs effectués chez les poissons selon des méthodes génétiques quantitatives. Sous ce rapport, les poissons ont sur les autres animaux d'élevage l'avantage de posséder un potentiel reproducteur relativement élevé et de faibles barrières à la reproduction.

Le maintien de stocks de poissons dans des habitats artificiels peut causer des changements génétiques indésirables, tels que perte d'hétérozygosité résultant de croisements consanguins et perte de santé. Nous indiquons des moyens de minimiser la consanguinité. Nous suggérons qu'on étudie les croisements entre eux de lignées consanguines et d'hybrides au sein de lignées et même d'espèces, afin de créer des niveaux élevés d'hétérozygosité et d'hétérosité ou vigueur des hybrides.

Accepted October 28, 1975 Accepté le 28 octobre 1975

[1]This paper forms part of the proceedings of a Symposium convened at the Harkness Laboratory of Fisheries Research, Algonquin Park, Ontario, October 1974, in honor of Professor F. E. J. Fry, M.B.E., M.A., Ph.D., D.Sc., F.R.S.C.

[2]Contribution No. 75-15 of the Fish and Wildlife Research Branch, Ontario Ministry of Natural Resources, Maple, Ont.

Printed in Canada (J4033)
Imprimé au Canada (J4033)

FISHERIES scientists have recently shown renewed interest in applying those quantitative genetic principles to aquaculture, including mariculture and pond culture, which have been used successfully in agriculture. Although commercial fish farmers and government hatchery biologists and managers have been selectively breeding their stocks for decades, methods of animal breeding based on the latest findings in quantitative and population genetics have been used only rarely. Recently, however, principally in Russia, Norway, Israel, Germany, and the USA, fisheries genetics programs have been initiated based on modern methods of animal breeding. Characters such as growth rate, resistance to certain diseases, morphological features, and temperature tolerance have been studied and in some cases manipulated by selective breeding and hybridization. In Ontario a cross between the lake trout (*Salvelinus namaycush*) and the brook trout (*Salvelinus fontinalis*) called the splake has been selectively bred for a number of years. This program received its initial stimulus from Dr Fry.

In order to discuss some aspects of selective breeding procedure, it may be helpful to develop a few basic concepts.

The phenotypic value of an individual P, can be expressed as the sum of the genotypic value G, and the environmental deviation E, i.e. $P = G + E$. So far in this symposium, the emphasis has been on the effect of the environment on the phenotype keeping the genotype constant. In selective breeding, the phenotype is manipulated by varying the genotype, usually keeping the environment constant. The variance of P, called the phenotypic variance, V_P, is equal to the sum of the genotypic variance V_G, and the environmental variance V_E, ignoring genotypic environmental correlation and interaction. It should be pointed out, however, that for fitness characters such as growth rate and survival, genotypic environmental interactions over a broad range of environments, such as hatchery and native, for example, have sometimes been found to be quite large. The genotypic variance can be expressed as the sum of components due to additive effects of the alleles, called the additive genetic variance, interaction among alleles at the same locus (dominance effects), and interaction among alleles at different loci (epistatic effects). Only the additive genotypic variance can be directly exploited by standard selective breeding techniques since the true breeding value of an individual is partially hidden by these dominance and epistasis interactions. The additive genotypic variance can be estimated from data on half sibs, full sibs, parents and their offspring, and inbred lines. The ratio of the additive genotypic variance V_A to the total phenotypic variance is called the heritability h^2, i.e. $h^2 = V_A/V_P$. Examples of estimates of heritabilities for fish are given below.

Species	Character	h^2
Splake hybrid	Early survival	0.76 (Ayles 1974)
" "	High temp resistance	0.38 (Ihssen 1973)
" "	Swimbladder gas retention	0.20 (Butler 1968)
Atlantic salmon	Resistance to vibrio disease	0.10 (Gjedrem and Aulstad 1974)
" "	Growth	0.60 (Lindroth 1972)
Carp	Weight of fingerlings	0.10–0.20 (Kirpichnikov 1966)

The importance of estimating V_A and hence h^2 lies in that the response to selection per generation, R, is proportional to the heritability i.e. $R = Sh^2$. S, the constant of proportionality, is equal to the selection differential as measured by the difference between the phenotypic means of the individuals selected and the whole population. The response to selection is usually expressed in terms of the selection intensity i, which is defined as S/σ_P, where σ_P is the phenotypic standard deviation. Thus $R = i\,\sigma_P h^2$ (Falconer 1967). For example, for swimbladder gas retention in splake $i \cong 1.3$, $\sigma_P \cong 4$ cm Hg, and $h^2 \cong 0.20$ (for explanation of units and experimental techniques of selection see Tait 1970). Hence $R \cong 1.0$ cm Hg per generation. After two generations of selection the actual gain was about 1.8 cm Hg compared to the expected gain of 2.0 cm Hg. In principle, one cannot predict the response to selection for more than one generation, because V_G and hence h^2 are altered after each selection. However, in practice it has been found that h^2 remains constant for several generations.

Many species of fish, including the salmonids, offer advantages over other livestock that have been selectively bred. Because of low reproductive barriers and ease of artificial cross-fertilization, interracial, interspecific, and even intergeneric hybrids have been produced. Hybridization makes it possible to combine several desirable characters in one strain or hybrid and to exploit hybrid vigor as has been done in agriculture (for a discussion of hybridization in fish see Butler 1968). The splake hybrid, in which desirable brook trout and lake trout characteristics are

combined, is an example of the foregoing. Also, because of the relatively high reproductive potential of most species of fish (compared to other livestock) the selection intensities can be very high, producing large selection responses per generation. For many commercially important species of fish, fertilization can be controlled to the extent of one's being able to produce complete diallel crosses, a technique in which n males and m females are crossed in all possible ways by separating the ova from each female into lots and fertilizing each lot with sperm from one of the n males. This experimental design, usually only possible for plants, is very efficient in estimating genotypic variance components, as well as parental effects.

Fisheries management programs, especially those that involve rearing fish in an artificial environment for at least part of their life cycle, can cause undesirable genetic changes. For example, some stocks of cultivated carp, in comparison to wild carp, have poor blood properties and lowered overall viability; and some domesticated trout strains have a shorter lifespan than the wild strain from which they were derived. Such genetic changes have to be considered not only for programs concerned with enhancing natural populations but also for strictly aquacultural programs where the maintenance of a special stock, produced by selective breeding or hybridization for example, is desired without further genetic change.

Natural populations have been shown to be immensely variable genetically (for a review see Lewontin 1974). For example, the average heterozygosity per locus for *Drosophila pseudoobscura* has been estimated to be about 35%. The question of how such a high level of genetic variability is maintained in a natural population has led to much debate and even heated controversy. It has been argued that balancing selection in which the heterozygote is of higher fitness than either homozygote can maintain high levels of heterozygosity. Hence, the mean fitness of the population depends on the level of heterozygosity. This view is supported by experiments that measure inbreeding depression, in which a loss in fitness correlated with a loss in heterozygosity is observed. However, I should point out that it has also been demonstrated (Crow and Kimura 1970) that the amount of heterozygosity observed within natural populations cannot be accounted for by balancing selection alone.

From a practical point of view, concern is with the change of the genetic makeup of fish populations due to management practices. For example, selective breeding programs in general have shown that increasing the heterozygosity of a stock is generally beneficial, whereas inbreeding with the consequent reduction in heterozygosity is generally harmful.

The main feature of fish culture techniques, especially for salmonids, is that under the protected environment of artificial rearing facilities, survival, primarily of early life stages, increases dramatically. In fact, natural selection is practically completely suspended with survival of over 90% not uncommon as compared to more than 90% mortality under natural conditions for the same period of the life cycle. This reduction in natural selection pressure can substantially decrease the level of heterozygosity for loci associated with survival in the natural environment. The following simple example illustrates this effect for one locus with two alleles A,a and relative fitnesses

AA	Aa	aa	
$1 - S_1$	1	$1 - S_2$,	$1 > S_2 > S_1 > 0$

where S_1 and S_2 are the coefficients of selection and the deleterious allele, a, is kept in the population by balancing selection. Then at equilibrium the amount of heterozygosity is given by

$$H = \frac{2S_1S_2}{(S_1 + S_2)^2}$$

and the average fitness advantage of the heterozygote by $\frac{S_1 + S_2}{2}$. If S_1 goes to zero so that the advantage of the heterozygote diminishes, and S_2 remains finite, H goes to zero. The debt in fitness accumulated by a stock in this way in a soft environment may well have to be paid back if it is returned to a more competitive environment.

Artificially propagated fish are usually the progeny of far fewer parents than wild fish are. The very efficiency of culture techniques allows one to maintain a relatively small brood stock compared to the number of offspring. The breeders themselves are sometimes derived from even fewer individuals representing a very small subsample of the natural population. Hence the genetic base of the population is very narrow especially if one also considers that the subsample of the native population was probably very far from random. Sex products of individual wild fish are usually collected in one geographical location at a specific time in the spawning migration or aggregation. This practice leads to a biased subsample of the gene pool of the native population since fish stocks are composed of temporal as well as spatially adapted subpopulations.

The proportion of heterozygotes remaining after t generations in a population of effective number N_i at generation i is

$$\prod_{i=0}^{t-1}\left(1-\frac{1}{2N_i}\right) \quad \text{(Crow and Kimura 1970)}$$

The effective number N_i is equal to the actual number of breeders if mating is random; equal numbers of males and females are used; the population is neither increasing nor decreasing; and the distribution of the number of progeny per mating is binomial.

If unequal numbers of males and females are used, as is usually the case for fish culture operations where fewer males than females are used, the effective number N_e is smaller than the actual, producing more rapid inbreeding. $N_e = \frac{4N_fN_m}{N_m+N_f}$ where N_m and N_f are the number of males and females, respectively.

The effective number as a function of the variation in family size is given by

$$N_e = \frac{N_{t-1}\bar{K}-2}{\frac{V_K}{\bar{K}}+\bar{K}-1} \quad \text{(Crow and Kimura 1970)}$$

where $\bar{K}$, V_K are the mean and variance in family size and N_{t-1} is the actual number at generation $t-1$. $N_e = N_{t-1}$ if the variation in family size is binomial. The variation in family size is larger than the binomial variance if for example a significant proportion of matings produces few or no progeny. This can occur if artificial fertilization is practiced since it is difficult in some species to pick females at their proper maturity. The equation also implies that the effective number cannot be increased by simply expanding the population size. Such a situation arises in hatchery production where large numbers of breeders are sometimes produced from a few parents. Suppose a hatchery population is derived from 2 males and 10 females chosen randomly from a large non-inbred population; and a brood stock of 300 females and 100 males is produced from these fish and maintained at this level for five further generations. The initial effective breeding population size is only 6.7 due to the disproportionate number of males and females. Hence the loss in heterozygosity in the first generation is about 7%. Assuming that the distribution in family size is binomial $N_t \cong N_{t-1}$ after the first generation and the loss in heterozygosity remains at about 7% per generation. After five subsequent generations the loss in heterozygosity is about 35%. Alternatively if the population had been started with 20 males and 20 females the loss in heterozygosity after five generations would have been only about 7%. Hence it is seen that most of the inbreeding can be avoided by starting with a larger base population.

Figure 1 shows the amount of inbreeding for several combinations of numbers of males and females assuming a binomial distribution in family size and keeping the size of the breeding population constant. It can be seen from the figure that the amount of inbreeding is primarily determined by the number of breeders of the minority sex. If full sibs are identified, as is the case for most selective breeding programs, the variation in family size can be reduced to zero by choosing the same number of breeders from each family for the next generation. In this case the effective population size is approximately doubled reducing the amount of inbreeding correspondingly. Figure 1 gives an example of this situation for various numbers of males and 50 females.

A more detailed description of the changing genetic makeup of a finite population is given by the distribution function of gene frequencies at different loci, viewing the change in gene frequency with time as a stochastic process. The change in gene frequencies solely due to the finite size of the population, quite apart from natural selection, caused by the random sampling of gametes (called random genetic drift) is being

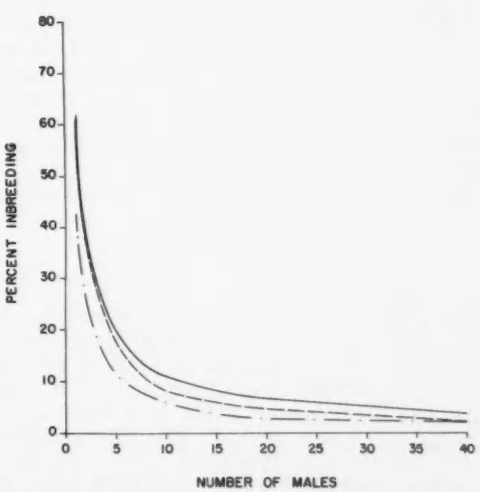

FIG. 1. Percent loss of heterozygosity after eight generations as a function of males and females. —— 50 females; – – – – – infinite number of females; –·–·–·– 50 females and variation in family size equal to zero.

considered, ignoring mutations and migration processes which can reintroduce genetic variability. The gene frequencies initially drift towards intermediate values until the distribution becomes approximately uniform. An increasing number of loci become fixed for a certain allele and eventually all loci become fixed. When a locus becomes fixed for one allele the other allele (or alleles) are lost from the population. The rate of fixation depends on the size of the population. For example, starting from a completely heterozygous population, i.e. every locus heterozygous, of effective size N, after 2N generations approximately 50% of the loci have become fixed.

Under the combined effects of mutation, selection, migration, and random drift the gene frequencies reach equilibria. The distribution in gene frequencies can be divided into three categories according to the size of the population (Fig. 2) (Wright 1932). These distributions can be viewed either as the frequency of a single allele at one locus among small breeding subgroups within the population or the frequency of alleles at different loci within one breeding group. With respect to mutations and migration, "small" (Fig. 2C) means $4N\mu < 1$ or $4Nm < 1$ where μ is the mutation rate, m the migration rate, and N the effective population size. 4Nm may not be small if the migrants make up a significant proportion of the population. Since natural mutation rates are usually of the order of 10^{-5}, mutations have a significant effect on the distribution for fairly large populations only. In a small population the gene frequency distribution is due to random processes and most genes are eventually either fixed or lost producing nonadaptive genotypes, because random deviation rather than selection determines the distribution. Also, the level of heterozygosity is smallest for the small population. The frequency of heterozygotes for a population in Hardy-Weinberg equilibrium for one locus is $2q\ (1 - q)$ where q is the frequency of the deleterious allele, which is maximum when $q = \frac{1}{2}$. For a small population, most frequencies are closer to zero or one (Fig. 2C) resulting in fewer heterozygotes. Fish populations managed intensively are usually of the small type and perhaps occasionally of the intermediate type.

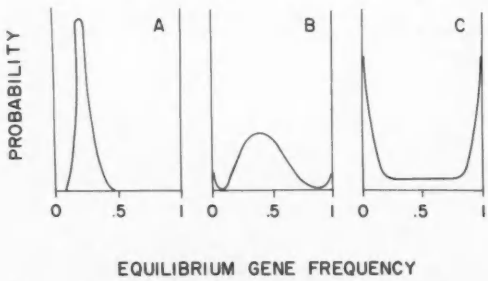

FIG. 2. Equilibrium gene frequency distributions for a large population A, one of intermediate size B, and a small population C (adapted from Wright 1932).

To maintain a fairly high level of heterozygosity and fitness in a stock the above discussion suggests several techniques. Besides preventing inbreeding as much as possible, mainly by starting and maintaining a large effective population size, further genetic variability can be introduced by crossbreeding and hybridization. In crop and livestock breeding the improved performance due to heterosis or hybrid vigor from crossbreeds and hybrids has been at least as important as the improved performance obtained by selective breeding. Crosses between inbred lines have been used to obtain vigorous hybrids in agriculture. Hybrid vigor is thought to be due to the heterozygosity at many loci for such hybrids. For some species of fish, such as rainbow trout, many breeds are available which could be hybridized and assessed for hybrid vigor. Also, wild races that are genetically isolated may be utilized in this way. However, inbred lines are not generally available for fish, and their production is slow because of relatively long generation times for most commercially important species. However, a short cut has been researched, namely diploid gynogenesis, in which eggs are fertilized with genetically inert spermatozoa. The zygotes are given a physical shock shortly after fertilization which doubles the number of maternal chromosomes, producing a normal diploid (Purdom 1970). Dr Fry has been interested in using high pressure as the physical shock to cause the doubling of the chromosomes. The offspring from fish produced in this way are highly inbred, and crosses between such breeds should show considerable hybrid vigor.

AYLES, G. B. 1974. Relative importance of additive genetic and maternal sources of variation in early survival of young splake hybrids (*Salvelinus fontinalis* × *S. namaycush*) J. Fish. Res. Board Can. 31: 1499–1502.

BUTLER, L. 1968. The potential use of selective breeding in the face of changing environment, p. 54–72. *In* K. H. Loftus [ed.] A Symposium on Introduction of Exotic Species. Ont. Dep. Lands For., Res. Rep. 82: 111 p.

CROW, F., AND M. KIMURA. 1970. An introduction to population genetics theory. Harper and Row, New York, N.Y. 591 p.

FALCONER, D. S. 1967. Introduction to quantitative genetics. Ronald Press, New York, N.Y. 365 p.

GJEDREM, T., AND D. AULSTAD. 1974. Selection experiments with Salmon 1. Differences in resistance to vibrio disease of salmon parr (*Salmo salar*). Aquaculture 3: 51–59.

IHSSEN, P. 1973. Inheritance of thermal resistance in hybrids of *Salvelinus fontinalis* and *S. namaycush*. J. Fish. Res. Board Can. 30: 401–408.

KIRPICHNIKOV, V. S. 1966. Effectiveness of mass and individual selection in fish breeding. Sov. Genet. 4: 11–17.

LEWONTIN, R. C. 1974. The genetic basis of evolutionary change. Columbia University Press, New York, N.Y. 346 p.

LINDROTH, A. 1972. Heritability estimates of growth in fish. Aquilo Ser. Zool. 13: 77–80.

PURDOM, C. E. 1970. Gynogenesis — a rapid method for producing inbred lines of fish. Fish. News Int. 9: 29–32.

TAIT, J. S. 1970. A method of selecting trout hybrids (*Salvelinus fontinalis* × *S. namaycush*) for ability to retain swim-bladder gas. J. Fish. Res. Board Can. 27: 39–45.

WRIGHT, S. 1932. The roles of mutation, inbreeding, crossbreeding and selection in evolution. Proc. VI Int. Congr. Genet. 1: 356–366.

A New Approach to Fisheries Management and F. E. J. Fry's Role in Its Development[1]

K. H. LOFTUS

Ministry of Natural Resources, Sport Fisheries Branch, Toronto, Ont.

LOFTUS, K. H. 1976. A new approach to fisheries management and F. E. J. Fry's role in its development. J. Fish. Res. Board Can. 33: 321–325.

Fisheries management has undergone a complex and tortuous process of development. From its initial stages as a largely intuitive activity, gradual incorporation of a biological basis has greatly strengthened its effectiveness. At present, there is considerable promise that a coherent, scientifically sound body of management science will soon emerge. The influence of F. E. J. Fry is inextricably associated with these developments.

LOFTUS, K. H. 1976. A new approach to fisheries management and F. E. J. Fry's role in its development. J. Fish. Res. Board Can. 33: 321–325.

La gestion des pêches s'est développée selon un processus complexe et tortueux. En grande partie intuitive dans ses phases initiales, elle a vu son efficacité grandement renforcée par l'incorporation graduelle d'un fondement biologique. On a présentement le ferme espoir qu'une science de gestion saine est sur le point d'émerger. L'influence de F. E. J. Fry est étroitement liée à ces développements.

Accepted October 28, 1975 Accepté le 28 octobre 1975

Some History

In the 1920s and 1930s the University of Toronto was the locus of interactions of a number of professors and graduate students who subsequently exerted a pronounced influence on Canadian fisheries science for a number of decades — perhaps as many as five. The current survivors are not an introspective lot: they are still far more interested in facing today's issues than in spending much time analyzing what it was about those earlier years that proved to be so stimulating. Apparently there was no single simple cause. Clearly there was no widely recognized scientific master who programmed them all to be his disciples: F. E. J. Fry has suggested that B. A. Bensley exerted a strong stimulus by setting up the Ontario Fisheries Research Laboratory and

[1]This paper forms part of the proceedings of a Symposium convened at the Harkness Laboratory of Fisheries Research, Algonquin Park, Ontario, October 1974, in honor of Professor F. E. J. Fry, M.B.E., M.A., Ph.D., D.Sc., F.R.S.C.

Printed in Canada (J4034)
Imprimé au Canada (J4034)

that W. J. K. Harkness's genius was to help young people to get started on interesting problems and then to arrange as much support and freedom as necessary (see also Dymond 1964). In retrospect these have clearly also been prominent aspects of Fry's genius during more recent decades.

Referring again to the Toronto generation of the 1920s and 1930s, half a dozen or more can be listed as each having excelled in a number of rather disparate aspects of fisheries science, aquatic biology, and management. Though generally in touch with each other, each apparently valued his independence to the point where they never organized attempts to interrelate their interests and inferences formally and explicitly. They were like pioneers strung out along a wide frontier. Of course there were numerous others besides Toronto graduates exploring the frontier — the point here is not to hail Toronto but to seek to understand events half a century ago and since.

The question of whether his scientific research was "pure" or "applied" never has had much meaning for Fry. It is far more important that he have as much freedom from administrative constraints as possible. His work on practical problems has included: the technique of "alternate closure of lakes to fishing to maintain attractively high rates of angler success" (Harkness and Fry 1942); the selectivity of gillnets (see Hamley 1975 for a comprehensive review); population estimates, in particular the approach of "virtual population" or "cohort analysis" that currently predominates in North Atlantic fisheries management (Fry 1949; Paloheimo 1961); the effect of annual temperature differences on reproductive success (see Christie and Regier 1973 for a review); the effect of thermal loading on inshore lake fish populations (Hurley 1975); as well as other initiatives treated by other authors in these symposium proceedings.

For the purposes of this paper another contribution is of particular interest. Many data on Ontario's fish and fisheries date from before the 1930s. For example, the catches of important species in various districts of the Great Lakes are available for the period since the Canadian confederation, 1867, and in some areas for several years preceding 1867. Also, a number of lakes and streams were surveyed, occasionally in some depth, in the first third of our century (Fry and Legendre 1963). The taxonomists of course gradually developed maps of species distribution (Scott and Crossman 1973). In the mid-1930s the data series on Algonquin Park lakes, particularly on Lake Opeongo was initiated (Radforth 1944). In the late 1940s the South Bay–Lake Huron data series was begun, and in the 1950s the Lake Ontario and Lake Erie series. Meanwhile in 1948 the collection, analysis, and banking of detailed catch records of Ontario's commercial fishermen was begun. Other series have been initiated since then and may not owe as much to Fry's direct stimulus as these others. These various data series contain highly valuable data in part because the variables that were selected for monitoring have turned out to have large information content. But it is true that most of the data have as yet been analyzed to only a very incomplete degree. To expedite further analysis is in fact one of the purposes of our recent initiative — the Ontario Fisheries Information System. But more of that later.

Though there can be no question that Fry's motivations to do fisheries research are to a large extent humanistic, that is clearly not his only basis for determining precisely which problems will receive his attention. He is perhaps equally motivated towards recognition and definition of principles and mechanisms of fish autecology, as well as towards refinement of the methods of ecological science. Perhaps it was this combination that led to his unique leadership role and direct productivity.

So What Went Wrong?

Since about 1960 Ontario's fisheries, particularly commercial fisheries, have been in crisis after crisis, each one more daunting than the last. One is tempted to suggest that there is little positive relation between the degree of scientific insight or the mass of data and the "amount of science" actually available to management. Some of the reasons lie outside the field of fisheries science per se — Regier and McCracken (1975) have argued that no ecological science however complete can have any definitive role in a management regime of the "common property–open access–willing consent type." Gradually this realization has grown and there is now sufficient recognition of it by politicians, civil servants, scientists, and fishermen to permit introduction of more workable approaches which have already ben tested here and there locally.

This kind of fundamental change in policy direction provides a great new opportunity for transfer of science into new management approaches and regulatory protocols. It is not enough now that researchers are very busy keeping up with new developments in narrowly circumscribed fields, as well as conducting and publishing their own work. Nor does it suffice that management people apply the science that they

learned 5, 10, or 20 yr ago as students. And we now have no confidence that some individual worker will be able to "hang it all together" informally and give the necessary and sufficient advice. Clearly researchers and managers must collaborate to bring together relevant insights and information, consolidate and publish it, communicate it to the public, and apply it in practice. To continue to close our eyes to this problem, or to bicker among ourselves about whose special responsibility it may be, will contribute to the further erosion of resources whose stewardship is our responsibility. And of course our credibility as professionals and individuals may disintegrate.

Recent Ontario Fisheries Management

Managers have been, and are, managing fisheries with varying degrees of success. Many agencies are currently reexamining their approaches to management, having become disenchanted with former and traditional methods and philosophies. Any new approach to fisheries management undertaken in this decade will inevitably, and fortunately, reflect aspects of the Fry paradigm. In Ontario, we are developing a new "approach to fisheries management." The details are currently being researched and debated by a federal–provincial working group on strategic planning for Ontario fisheries.

During the decades up to and including the 50s, research people were concentrating, for the most part, on learning about and documenting the natural history of the more important fish species. Physiological ecology — how the animals work internally, and how the aquatic environment might limit animal numbers and distributions — had its beginning. Research people also began work on population dynamics at about this time. The results of this research have now been so well integrated in our science that their origin is seldom recognized. None of these basic components of our science are yet complete, though the necessary continued work on them no longer creates much excitement.

Fisheries management, during this period, consisted essentially of two unwedded operations: law enforcement and fish culture, both of which were founded primarily on the conviction that motherhood was a good thing. Management-oriented biologists began to appear in the late 40s and 50s and promptly made themselves unwelcome by questioning the biological basis for many of the laws, and by questioning the value of planting fish. Much of the new management biologists' energy was dissipated in that they had to defend against ad hominem attacks, both from inside and outside government, that questioned their motives, intelligence, sanity, etc. Nevertheless, they did manage to establish and to maintain a "bridgehead," and to bring some improvements to both the hatchery and legislative programs. They also adapted the lake or stream survey as a useful means of checking on complaints of poor fishing locally. While, in retrospect, it is easy to suggest that these surveys were poorly done, poorly documented, and seldom provided a sufficient basis for diagnosing a lake problem, nevertheless, they did contribute to the emergence of public confidence in management, and they did establish some excellent "point-in-time" reference data, for which we continue to be thankful.

In general, work was concentrated upon single species. Waters were considered unique, that is, no two water bodies could be taken as replicates for practical purposes. The overall supply of fish appeared to exceed the demand. After early intensive work in the period 1880–1900, biologists had apparently lost their awareness of water quality degradation and of its impact on fish. This was the fertile ground upon which "liberalization" flourished in Ontario. So much for the 40s and 50s.

The 1960 decade was a difficult one for fisheries people. D.D.T. and various other substances found a new and important place in the fisheries literature, not just as a contaminant in fish, but as contaminants throughout the aquatic ecosystem, and more importantly perhaps, as examples of what might be the impact of other exotic chemicals. Also in the 60s, water quality degradation rapidly became extreme in larger areas adjacent to major cities and industries and we became fully aware of its impact on the traditionally important species. Limnological literature relating to water quality and productivity blossomed. Physiologists concentrated their work on lethal and sublethal levels of contaminants and on the effects of the components of nutrient loading on fish. Parts of water such as Lake Erie had become anaerobic yet the overall productive capacity seemed unchanged. Species dominance was changing, not just in over-rich Lake Erie, but in "unpolluted" Lake Ontario and in lakes Huron and Michigan. We began to recognize secondary and long-term effects resulting from the invasion of fish communities by species such as the sea lamprey, smelt, and alewife. Suspicions of overexploitation again grew and with the reexamination of the vital statistics of catches the significance of the "fishing-up" process emerged more clearly. The literature was stimulating and warm debates arose among research people, but

it was a very confusing and frustrating literature for the managers who could discern no clear alternative to continuing to operate as they had in the past, only to do it better.

Supplies of premium fish stocks declined. Demands for fishing opportunities increased. A new initiative for management was clearly necessary, but just as clearly was not available.

A New Initiative

The confusion of the 60s, though stimulating, was in the end as bothersome to the research people as it was to the managers. There emerged in the late 60s and early 70s a sense of urgency to consolidate and synthesize the available knowledge in order to find, if possible, a fresh perspective for developing new approaches for both research and management. The Symposium on Salmonid Communities in Oligotrophic Lakes (SCOL) conceived in the late 60s and held in 1971 (Loftus and Regier 1972) was an important learning experience. To the extent that a 1968 Fisheries Research Board grant on aquatic community and ecosystem ecology to a group of University of Toronto biologists was an important precursor and supporter of the SCOL symposium, F. E. J. Fry's special contribution may be noted. He was the first among the Toronto group to support a proposal to apply for FRB support on that topic.

A number of generalities emerged from the SCOL exercise, among them the following.

1) Three categories or groupings of man-induced stresses on fish populations have particularly marked effects: exploitation; artificially induced and accelerated enrichment; and species introductions, intentional or otherwise. Shoreline modifications, poisons, siltation, and contaminants are usually of secondary importance from the viewpoint of impact on the ecological system.

2) Each of the major stresses appears to drive salmonid populations in the same direction, i.e. towards collapse, if the extent of stress is allowed to increase and increase. It usually has been. In combination, two or more of the stresses appear to be, at least, additive, and more likely synergistic.

3) The response of the fish community of species to severe stress may not be fully expressed for decades — in fact that response may be continued instability of populations the details of which appear to be unpredictable. Regier (1973) has tentatively identified a "general adaptation syndrome" to major stress which involves a shift in the direction of smaller pelagic species and forms, which have low self-regulatory capability, and thus fluctuate erratically. This syndrome is defined at the community level of organization.

4) The symptoms of response by fish to stress are probably sequential and typical: i.e. increased growth rate, increased fecundity, modified year-class structure in the population, increasing fluctuation in year-class strength, increasing failure of recruitment, etc. This might be termed a general adaptation syndrome at the population level.

5) The response to stress may not necessarily appear first in the top predator of the community. If this is so, then one must monitor the community, not just one species, in order to detect the earliest responses to stress.

6) Salmonid communities, and/or oligotrophic lakes appeared amenable to treatment as a "set." It therefore seems unnecessary that we continue to be boggled by the former preconception that each lake and each fish community is a fundamentally different entity. If one set can be recognized as useful in a management and research sense, surely other sets can be similarly recognized.

7) The most useful "case histories" in the SCOL synthesis were those with data series of longest term. In the absence of definition of critical stress levels, "trend-through-time" data were essential for understanding the sequence of events.

Other tentative inferences could be listed but those above are perhaps adequate for our purpose here. These and others ought to be carefully tested, and can be, using existing data from other waters.

The federal–provincial strategic plan for Ontario fisheries is not yet fully developed, but it seems clear that a more comprehensive Ontario Fisheries Information System (OFIS), with rapidly and fully accessible data stores, will be essential for the effective implementation of the strategic proposals, as well as for testing and transferring into practice the above ideas.

OFIS

The main priority of OFIS will be trend-through-time data. More traditional point-in-time survey data will of course also be incorporated. A library of maps, as detailed as is practicable, is an essential component. The primary variables to be monitored concern fish harvests, fish habitat, fish community, and resource users. For each class a series of more specific variables is being defined.

In Ontario it is clear that we cannot hope for the financial and/or staff support required to

gather data frequently on all our waters which number in the hundreds of thousands. We will concentrate on major and representative waters across the province. Representative waters are being designated on the basis of trophic status and/or fish community, and by recognized gross stress level. Major waters include the Great Lakes, Simcoe, Nipigon, Nipissing, Lake of the Woods. Perhaps two or three sets of type lakes each consisting of perhaps six lakes, in each of eight administrative regions, will be selected. The traditional survey approach which provides "point-in-time" data, an important component of our ongoing management effort, will be much more amenable to interpretation when they can be compared to "trend-through-time" data series available for similar waters within the same region.

The foregoing is the Ontario approach to a fisheries information system. It has been accepted in principle by Cabinet as a new initiative and has been partially funded and staffed during 1974–75. We are proceeding with the major tasks of identifying sets of lake types, and of identifying and generally quantifying the parameters of our "trend-through-time" data base. Achievement of a fully operational OFIS for the province should provide a much enhanced opportunity for research, for experimental management, and for more effective regulation.

Postscript

Not long ago, having thought this business through, I sought an occasion to try it out on F. E. J. Fry to get his reaction and comment. When the occasion arose and when I was about to introduce the subject, Fry interjected with something like, "you know, what we need in Ontario are some really good biological surveys." A little probing demonstrated that he was thinking of "trend-through-time" data series.

How do you get ahead of this guy?

Acknowledgments

The colleagues who contributed to the emergence of this new approach to management are too numerous to list. The effort of Dr H. A. Regier in manuscript revision was especially helpful.

CHRISTIE, W. J., AND H. A. REGIER. 1973. Temperature as a major factor influencing reproductive success of fish — two examples. Rapp. P.-V. Reun., Cons. Int. Explor. Mer 164: 208–218.

DYMOND, J. R. [ed.] 1964. Fish and wildlife. A Memorial to W. J. K. Harkness. Longmans Canada Limited, Toronto, Ont. 214 p.

FRY, F. E. J. 1949. Statistics of a lake trout fishery. Biometrics 5: 27–67.

FRY, F. E. J., AND V. LEGENDRE. 1963. Ontario and Quebec, p. 487–519. *In* D. G. Frey [ed.] Limnology in North America. Wisconsin University Press, Madison, Wis.

HAMLEY, J. M. 1975. Study of gillnet selectivity: a review. J. Fish. Res. Board Can. 32: 1943–1969.

HARKNESS, W. J. K., AND F. E. J. FRY. 1942. Game fish management in Algonquin Park lakes. Trans. North Am. Wildl. Conf. 7: 398–404.

HURLEY, G. V. 1975. The reproductive success and early growth of smallmouth bass, *Micropterus dolomieui* Lacépède, at Baie du Dore, Lake Huron, Ontario. M.Sc. Thesis. Univ. Toronto, Toronto, Ont. v + 149 p.

LOFTUS, K. H., AND H. A. REGIER. [ed.] 1972. Proc. Symp. on Salmonid Communities in Oligotrophic Lakes (SCOL). J. Fish. Res. Board Can. 29: 613–986.

PALOHEIMO, J. 1961. Studies on estimation of mortalities. I. Comparison of a method described by Beverton and Holt and a new linear formula. J. Fish. Res. Board Can. 18: 645–662.

RADFORTH, I. 1944. Some considerations on the distribution of fishes in Ontario. Contrib. R. Ont. Mus. Zool. 25: 116 p.

REGIER, H. A. 1973. The sequence of exploitation of stocks in multi-species fisheries in the Laurentian Great Lakes. J. Fish. Res. Board Can. 30: 1992–1999.

REGIER, H. A., AND F. D. MCCRACKEN. 1975. Science for Canada's shelf-seas fisheries. J. Fish. Res. Board Can. 33: 1887–1932.

SCOTT, W. B., AND E. J. CROSSMAN. 1973. Freshwater fishes of Canada. Bull. Fish. Res. Board Can. 184: xi + 965 p.

Initiation of Sea Lamprey (*Petromyzon marinus*) Control[1]

W. M. SPRULES
Ottawa, Ont. K1H 7N9

SPRULES, W. M. 1976. Initiation of sea lamprey (*Petromyzon marinus*) control. J. Fish. Res. Board Can. 33: 326–329.

Sea lamprey (*Petromyzon marinus*) control became a major undertaking, relative to many other programs in aquatic biology. In several respects, the history of the program, outlined here, provides an informative prototype that might be usefully considered by aquatic biologists. F. E. J. Fry played an influential role in the development of the program.

SPRULES, W. M. 1976. Initiation of sea lamprey (*Petromyzon marinus*) control. J. Fish. Res. Board Can. 33: 326–329.

Par comparaison avec plusieurs autres programmes de biologie aquatique, le contrôle de la lamproie marine (*Petromyzon marinus*) est devenu une opération majeure. Sous bien des aspects, l'historique du programme esquissé ici fournit un prototype de renseignements que les biologistes des eaux auraient intérêt à étudier. F. E. J. Fry joua un rôle important dans le développement du programme.

Accepted October 28, 1975 Accepté le 28 octobre 1975

Initiation of Sea Lamprey Control

The rapid spread of the parasitic sea lamprey (*Petromyzon marinus*) throughout the upper Great Lakes in the late 1930s and 1940s created fishery management problems of an order of magnitude hitherto unknown in this extensive freshwater system. As lamprey populations became established in Lake Michigan, Lake Huron, and Lake Superior, respectively, their effect on species of sport and commercial interest became apparent through the increasing number of old and new lamprey scars observed on larger fish in the catches, and the drastic decline in annual production of certain valuable species such as lake trout. Fishermen, conservationists, and fishery scientists became very vocal in expressing deep concern for the future of the important historic fisheries of this area if effective lamprey control measures were not introduced immediately.

The timing of these events was unfortunate because it coincided with the war years from 1939 to 1945 when new funds and additional personnel could not be obtained to initiate programs which would have to be classified as nonessential under the circumstances. As public concern increased, all levels of government became aware of the magnitude of the problem and recognized that international cooperation was essential because hundreds of miles of international boundary between Canada and the United States extended throughout the Great Lakes system. Further, in one way or another, legislative and administrative responsibility for the fisheries fell within the purview of the two federal governments, the Government of Ontario and the governments of the several states bordering the Great Lakes.

Following the cessation of hostilities in 1945, governments were in a position to set new priorities and representatives of the governments of Canada and the USA drafted and signed a Great Lakes Fishery Treaty in 1946. Canada was prepared to ratify this treaty but the formal exchange of ratifications did not occur because certain state governments objected to the treaty articles granting authority to an international commission to regulate fisheries in the Great Lakes.

Although this treaty did not enter into force, the data on the condition of the Great Lakes fisheries which were presented during the negotiations showed how serious the situation was and sufficient support for immediate action was obtained to establish a Great Lakes Sea Lamprey Committee later in 1946. This Committee was combined subsequently with a similar Lake Trout Committee and functioned as a Great Lakes Fishery Committee from 1953 to 1957. These committees were composed of representatives from the U.S. Fish and Wildlife Service, agencies of the several state administrations bordering the Great Lakes and the Ontario Department of Lands and Forests. Thus, although the interna-

[1]This paper forms part of the proceedings of a Symposium convened at the Harkness Laboratory of Fisheries Research, Algonquin Park, Ontario, October 1974, in honor of Professor F. E. J. Fry, M.B.E., M.A., Ph.D., D.Sc., F.R.S.C.

Printed in Canada (J4035)
Imprimé au Canada (J4035)

tional negotiations had fallen short of the goal envisaged, a forum had been established where information and ideas could be exchanged and cooperative programs of lamprey investigation and control, as well as fisheries management, could be undertaken through mutual agreement. During the period from 1946 to 1953 the interested agencies gathered and exchanged information on the life history, distribution, and abundance of sea lamprey and on the condition of the fish stocks supporting the major fisheries in the Great Lakes.

Data obtained from the early lamprey studies in the upper Great Lakes showed the concentration and vulnerability of adult lamprey as they entered tributary streams during the spawning run. It was obvious that a large measure of control could be realized if spawning lamprey could be prevented from reaching the upstream spawning areas. Although there were many sceptics, increasing support for some kind of control program developed and by 1948 and 1949 the U.S. Fish and Wildlife Service began to conduct field tests of mechanical and electrical barriers which could be installed in major lamprey spawning streams to obstruct the runs. The results of these field tests showed very clearly the enormous scope of the control program required, the devastating effect of lamprey predation on certain fish stocks, and the continuing spread and buildup of lamprey in the upper Great Lakes. In addition, it appeared that minor modifications in design and operation would provide a reasonably effective and practical control mechanism.

Government officials in Washington, D.C. advised officials in Ottawa early in 1952 that the major problems which prevented the U.S. government from ratifying the 1946 treaty had been resolved and that they were prepared to reopen negotiations at an early date. Representatives of the two governments met late in 1952 and again early in 1953 to draft a mutually acceptable Great Lakes Fishery Treaty. Although agreement was reached on all nonoperative articles and on many operative articles, the negotiations were broken off by Canada when it became clear that the United States could not agree to including provision for fishery research in all the Great Lakes within the terms of the Treaty. During the next few months the respective negotiators received new instructions and the Convention on Great Lakes Fisheries as we know it today was negotiated and signed in the fall of 1954. This Convention was ratified by the governments of Canada and the United States on October 11, 1955 and the Great Lakes Fishery Commission, established under the terms of the Convention, held its oragnizational meeting early in 1956.

The Commission established its headquarters at the University of Michigan in Ann Arbor and appointed an acting Executive Director. From this time on the Commission assumed responsibility for development of a program to eradicate or minimize sea lamprey populations in the Great Lakes and for formulation of a research program to determine the need for measures to make possible the maximum sustained productivity of fish stocks of common concern. The success of the Commission's lamprey control program, which was begun in Lake Superior and extended to the other Great Lakes as methods were refined and funds became available, has been documented in the Technical Report Series and other publications of the Commission.

In the period between 1953 and 1956, when the Commission assumed responsibility for lamprey control, national programs were initiated in Canada and the United States and coordinated by the Great Lakes Fishery Committee referred to earlier in this paper. At the time of the unsuccessful treaty negotiations in 1953 it was obvious from the technical reports submitted to the conference that the United States was well ahead of Canada in developing and testing potential lamprey control devices and in knowledge of the size and location of spawning runs in U.S. streams entering the upper Great Lakes. A major factor contributing to this situation was probably the disastrous collapse of the lake trout fishery in Lake Michigan which lies entirely within U.S. territory. Electrical barriers to control lamprey spawning runs in U.S. streams entering the eastern end of Lake Superior were to be constructed in 1953. In order to cooperate in this program and to maintain a strong bargaining position for the next round of treaty negotiations, Canada initiated a similar program to begin in the eastern end of Lake Superior and extend westward as required.

A Federal–Provincial Great Lakes Fishery Research Committee was established in June, 1953 with equal representation from the federal Department of Fisheries and the provincial Department of Lands and Forests. One of the committee's responsibilities was to develop the lamprey control program in Canadian waters. Federal funds were made available to augment the provincial allotment for fishery studies in the Great Lakes and top priority was given to stream surveys and barrier construction in streams entering Lake Superior between Sault Ste. Marie and Montreal River Harbour. Dr Fry, our guest of honor at this symposium, was a member of this committee and his knowledge, enthusiasm, and candidness contributed significantly to many of the early, important decisions reached. The com-

mittee was unable to obtain the immediate services of a full-time director, although offers were made to several scientists possessing the required qualifications, and codirectors were appointed from the committee membership (Dr Fry and Dr Sprules) as an interim measure. Fortunately, Dr J. M. Speirs agreed to assume the responsibilities of secretary and field general for the codirectors and a small staff of biologists, engineers, and technicians was obtained through appointment or secondment.

In the early stages of the field program, streams entering Lake Superior between Sault Ste. Marie and Montreal River Harbour were surveyed to determine the presence of sea lamprey and to locate the most suitable site for construction of a barrier to the upstream migration of spawning lamprey. Electrical barriers, similar to those developed and operated by U.S. agencies, were installed as soon as the necessary site clearances were obtained and access roads constructed, and the lamprey control program in Canadian waters was underway.

Although many construction and operation difficulties were avoided as a result of advice and field assistance received from our U.S. colleagues, the operation of each new barrier seemed to introduce new problems. The theory of lamprey control by the use of electrical barriers seemed simple enough. All that was required was a network of fully effective barriers which would prevent all spawning adults from reaching spawning areas suitable for the survival of eggs and larvae. However, in practice control of lamprey by the use of electrical stream barriers proved very difficult. The major problem was to maintain an effective, uninterrupted electrical field in all spawning streams throughout the full period of the spawning migration. As would be expected, the operations were interrupted on occasion as a result of generator or line power failure, spring and flash floods causing high water levels, heavy currents, and physical damage by floating debris, and human interference. In addition, there were certain side issues requiring attention such as the safe passage of spawning runs of desirable fish species and provision for the upstream movement of boats in streams designated as navigable waters. As experience was gained, both the barrier design and operation were modified and the efficiency of the program increased significantly.

The Canadian and U.S. national programs in the upper Great Lakes were extended each year and all Lake Superior tributaries, 1293 in the USA and 622 in Canada, had been surveyed by 1956 when the Great Lakes Fishery Commission assumed responsibility for lamprey control. At this time 48 barriers had been constructed and operated in the USA and 33 in Canada. In addition, at least cursory surveys had been made of all Lake Michigan and Lake Huron tributaries and 19 barriers constructed and operated in Lake Michigan and two in Lake Huron including one in Canada and one in the USA.

The rapid accumulation of data on sea lamprey life history and behavior at the electrical barriers showed that the level of control considered essential for restoration of the traditional lake fisheries would prove very expensive and perhaps impossible to attain. Although thousands of lamprey were killed at the barriers each year, many escaped and reached upstream spawning areas when the barrier operation was interrupted. New runs appeared in streams where barriers had not been constructed and sea lamprey larvae were found in shallow inshore areas of Lake Superior at the mouths of major spawning streams. However, the most serious deficiency in the electrical barrier control method was the failure to eliminate downstream migrating larvae and transformed adults. It had been found that the larval stage lasts from 3 to 10 yr in the streams and thus the adult stocks in the lakes would be replenished annually for several years after barrier operation affected the success of spawning runs. The need for a control method designed to eliminate the larval accumulation in spawning streams was obvious.

The second phase in the lamprey control program was initiated by the Great Lakes Fishery Commission in 1958 when selected spawning streams were treated with a chemical lampricide. More than 6000 chemicals were tested in laboratory experiments conducted by U.S. scientists before the decision was reached to field test the chemical T.F.M. (3-trifluoromethyl-4-nitrophenol). The field tests proved successful and a program of stream treatment, followed by retreatment as required, was introduced. Each chemical treatment reduced or eliminated the larval accumulations in the streams and electrical barriers became obsolete as control devices. A few barriers continue in operation to assess changes in the size of spawning runs to specific streams. The chemical control method is still in use and the program has been extended to include all the Great Lakes.

This Symposium on the Fry Paradigm has brought together many scientists who have played an active role in research and management of the Great Lakes fisheries and are familiar with the lamprey control program. I hope those of you who have not been directly associated with the Great Lakes fisheries and feel a need for more

detail concerning the sea lamprey control program, will review the appropriate publications of the U.S. Fish and Wildlife Service, Fisheries Research Board of Canada, and the Great Lakes Fishery Commission or direct your queries to the experts who attended the Symposium.

The invasion of the upper Great Lakes by the sea lamprey will be classified as a disaster, at least for some time. However, some real benefits have accrued including international cooperation in fisheries between Canada and the USA; federal–provincial cooperation in fishery research and development in Ontario; and Dr Fry's increased interest in all Great Lakes fishery problems. It is hoped that our distinguished guest of honor will continue to serve as a Canadian Commissioner on the Great Lakes Fishery Commission for many years and that his well-earned retirement from the University of Toronto will not prove to be a limiting factor in the continuing development of Great Lakes fisheries.

Ecological Analysis and the Fry Paradigm[1,2]

S. R. KERR

Ontario Ministry of Natural Resources, Fish and Wildlife Research Branch, Maple, Ont. L0J 1E0

KERR, S. R. 1976. Ecological analysis and the Fry paradigm. J. Fish. Res. Board Can. 33: 329–332.

Appreciation of the essential distinction between internal and external methods of analysis is a fundamental component of the Fry paradigm. Investigation of the emergent behaviors of systems, observed at several hierarchical levels of ecological organization, is emphasized in his work. Internal analysis is always preceded by observation of the relevant external variables. The value of this approach is clear when assessed in terms of recent developments in systems theory.

KERR, S. R. 1976. Ecological analysis and the Fry paradigm. J. Fish. Res. Board Can. 33: 329–332.

Une connaissance de la distinction essentielle entre les méthodes internes et externes d'analyse est une composante fondamentale du paradigme de Fry. Ce dernier met l'accent, dans ses travaux, sur l'investigation du comportement qui émerge des systèmes, observé à plusieurs niveaux hiérarchiques de l'organisation écologique. L'observation des variables externes pertinentes précède toujours l'analyse interne. On se rend compte de la valeur de cette approche quand on l'évalue en termes des récents développements dans la théorie des systèmes.

Accepted October 28, 1975 Accepté le 28 octobre 1975

DEVELOPMENT of an established scientific field is shaped by the underlying conceptual outlook that is shared by its investigators. Advent of a new conceptual outlook or paradigm can quite substantially redirect a field from its established patterns (Kuhn 1970). Several paradigms have shaped the development of ecology in recent decades. A major purpose of this symposium is to identify and assess one such fundamental outlook — the Fry paradigm.

For my contribution to this purpose, it is convenient to begin with a seemingly different paradigm. The systems paradigm is now commonplace in ecological analysis. My intention is to show that the Fry paradigm can be usefully understood in that context.

A priori, it is necessary to discuss two systems properties that are generally attributable to biological assemblages. Emergent behavior comprises one such property, which is itself most easily approached through the property of hierarchical organization.

We quite generally recognize that biological

[1]This paper forms part of the proceedings of a Symposium convened at the Harkness Laboratory of Fisheries Research, Algonquin Park, Ontario, October 1974, in honor of Professor F. E. J. Fry, M.B.E., M.A., Ph.D., D.Sc., F.R.S.C.

[2]Contribution No. 75-14 of the Fish and Wildlife Research Branch, Ontario Ministry of Natural Resources, Maple, Ont.

Printed in Canada (J4036)
Imprimé au Canada (J4036)

systems exhibit hierarchical organization. The familiar organizational spectrum from individual organisms through populations to communities is one such example of hierarchy that is commonly used in text books. The notion of hierarchy doubtless seems natural to us because human social structures are unfailingly organized in that way.

The idea of emergent properties follows readily from the notion of hierarchy. It is clear that additional structural and functional properties become evident as we traverse an organizational hierarchy through levels of increasing complexity. Some properties emerge in obvious ways: thus, an individual cannot ordinarily be said to have a mortality rate, but its population can. Other emergent properties, for example genetic epistasis, as discussed earlier in this symposium by Dr Ihssen, can be considerably more difficult to understand. The property of being alive is perhaps one of the most difficult. A cadaver can usually be distinguished from a living organism without much difficulty, but the precise distinctions, nevertheless, pose serious problems in some contexts, as with the complex ethical problems associated with human organ transplants. In the latter instance, I believe that the difficulties do not so much arise from our limited understanding of the organic processes that are necessary to sustain life, but rather because we lack unequivocal criteria for agreeing when life can be said to occur.

There are many kinds of emergent properties that occur, or that we suppose to occur, in ecological systems; properties such as diversity, stability, trophic level, and the like. Parenthetically, notice that these terms tend not to occur very much in the Fry paradigm, Notice also that these terms tend to bring various difficulties to mind. I suggest that a major part of the difficulties we associate with these terms lies primarily in the problems we experience in observing and defining these as unequivocal emergent properties, in the sense of closed, single-valued transformations, or their stochastic equivalents.

Analysis of Ecological Systems

To justify why I think we have difficulty with emergent ecological properties, it is helpful to consider how we study systems of any kind. We of course begin by observing variables: there is no scientific alternative. In operational terms, there are exactly two general methods of analysis that can be applied to selecting the appropriate variables for observation. As Rosen (1969) has pointed out, one method entails devising an "internal" description of the system variables, in the form of mechanistic representation of selected system components, together with their relevant interactions. This method is frequently used by ecologists (as with Beverton and Holt, Volterra, and other familiar examples).

The second method of analysis is that of "external" description, framed in terms of output variables that describe selected behaviors of the intact system. In many cases, but not necessarily, the output variables are observed in relation to various kinds of inputs impressed upon the system, inputs such as environmental factors. There are many ecological examples of this kind of analysis: at the organismic level of organization, Fry's various environmental factors studies; at the population level, Fry and Watt (1957); and at the community level, Ryder (1965) serve as illustrations.

I have stressed that there are but two different ways of analyzing systems: the "internal" method, and the "external" method. Granted the hierarchical structure of ecological systems, these of course differ in operational terms only, but the distinction is, nevertheless, crucial. Essentially, the variables that we observe can be chosen either as emergent system variables, or as suites of internal variables.

The distinction becomes important when we recognize that "real" objects of any kind possess an unlimited number of variables that are potential candidates for observation: the problem is, therefore, one of selection. Faced with an unlimited number of variables, together with a corresponding number of possible interactions among these, the problem of adequate system description is clearly intractable unless the representation or model of the system can be formulated so as to encompass some appropriate subset of possible system behaviors. It is my contention that appropriate selection of variables is quite unlikely unless a satisfactory description of the system is first derived in terms of its emergent system properties. That is, successful internal analysis of a system is necessarily preceded by observation and theory at the external level of analysis.

I can offer some examples in support of this contention. The current debate over the popular stability–diversity hypothesis affords a good illustration of trying to reason, ineffectively in my view, from internal descriptions to emergent behaviors. Effective analysis, according to my reasoning, must proceed in the opposite direction. As Goodman (1974) points out, stability is not so much something we unequivocally observe in ecological communities, it is rather something that we seem to think should occur, perhaps be-

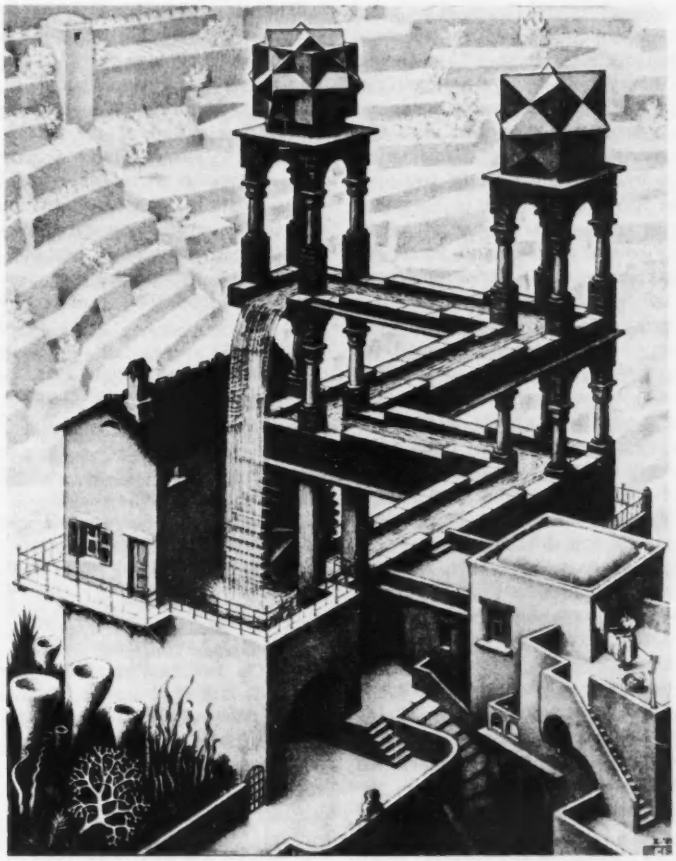

FIG. 1. "Waterfall," by M. C. Escher. Reproduced by permission, Escher Foundation–Haags Gemeentemuseum, The Hague. For analysis, see text.

cause the notion appeals to us for cultural reasons. There is surprisingly little available in the way of unequivocal observation of ecological stability, despite the fact that at least two major conferences dealt with the subject in recent years.

In short, it is my view that current stability theory is based largely upon internal analysis, without effective recourse to observation of the appropriate external variables. Confirmation of this view comes from stability theory itself, which is largely predicated upon the generalized species interactions embodied in the Lotka-Volterra equation (e.g. May 1973). Considering that species interactions comprise a small subset of the internal processes that we know to be "stabilizing" in one or another sense, and considering that there are an unlimited number of other internal variables that could be incorporated in a given model (spatial and temporal heterogeneities; other system components such as "decomposers" are some we know to be relevant in this context), it is hardly surprising that the sometimes elegant analyses that we call stability theory should have reached a sterile conclusion. We have learned a great deal about the properties of a certain type of equation; but we have learned relatively little, in my view, about ecosystems.

I have strongly criticized current stability theory: lest this be mistaken for my major point, note that many other examples could have served as well to illustrate my argument. Stability theory was selected solely because it is a popular subject and therefore widely known. The salient point is that by taking a collection of internal properties, and examining their aggregate behavior, without making recourse to the emergent

behaviors of the intact system itself, it is quite likely that erroneous conclusions will be reached.

Recognizing that the illustration I have chosen from ecological theory may have emotional ties for some of you, I shall provide a second example chosen from a nonecological discipline that will, I hope, provide us with an objective confirmation of my thesis. The hydrodynamic model provided by Escher, in the form of Fig. 1, is not without intrinsic interest in these times of energy crisis. But alas, Escher's general conclusion is forbidden by the laws of thermodynamics. Notice, however, that the artist's conclusion was cleverly attained by exactly the process that I have been discussing: seemingly correct combinations of selected internal properties that result in an unacceptable emergent conclusion. Technically speaking, the artist's tactics differ slightly from the methods of ecological modelling, in the sense that Escher has taken a subtle liberty with the laws of perspective in the process of mapping a system that is proposed to exist in 3-space onto the model constraints of 2-space. But this difference, I argue, is trivial. Ecological analysis inevitably involves mapping from an n-dimensional reality to a greatly simplified representation: the only real distinction, therefore, concerns the emergent laws that may be violated during the process of simplification. I trust the point is taken that in Robert Rosen's words, "observation and theory at the higher organizational level necessarily precedes effective synthesis at the lower organizational level" (Rosen 1969).

I suggest that we are going to need much more in the way of observation, and theory based on observation, at the higher organizational levels before we can develop effective internal explanations of ecological processes.

Much of what I have said has been critical and negative. My rationale is that I could not so easily illustrate my thesis with positive examples, although these of course exist in abundance in the ecological literature.

The Fry Paradigm

Rather than take up your time with positive illustrations, simply for the sake of symmetry, I return instead, briefly, to my initial point. As my contribution to our joint task of unravelling the Fry paradigm, I draw your attention to the remarkably consistent and productive manner in which Dr Fry's work has dealt with the emergent behaviors of the biological systems he studied. Whenever internal analysis appears in his work, it is always subsequent to identification of the relevant emergent properties.

This, I submit, is no coincidence, despite the fact that it first occurred in his work long before the current development of systems analysis that now makes such observations easy. Instead it is a deep and thoughtful consequence of relying on direct observation of the integral system at all stages of a study. The Fry paradigm, in short, does not seem to rely very much on armchair contemplation of natura naturans. In my view, this is the central concept of the Fry paradigm.

The only remaining question, in my mind, is whether Dr Fry agrees with me in this analysis, quite apart from the rest of you.

FRY, F. E. J., AND K. E. F. WATT. 1957. Yields of year classes of the smallmouth bass hatched in the decade of 1940 in Manitoulin Island waters. Trans. Am. Fish. Soc. 85: 135–143.

GOODMAN, D. 1974. The validity of the diversity-stability hypothesis. Proc. Int. Congr. Ecol. 1: 75–79.

KUHN, T. S. 1970. The structure of scientific revolutions. 2nd ed. Int. Encycl. Unified Sci. 2: 210 p.

MAY, R. M. 1973. Stability and complexity in model ecosystem. Monographs in population biology No. 6. Princeton University Press, Princeton, N.J. 235 p.

ROSEN, R. 1969. Hierarchical organization in automata theoretic models of biological systems, p. 179–199. *In* L. L. White, A. G. Wilson, and D. Wilson [ed.] Hierarchical structures. American Elsevier Publishing Co., Inc., New York, N.Y. 322 p.

RYDER, R. A. 1965. A method for estimating the potential fish production of north-temperate lakes. Trans. Am. Fish. Soc. 94: 214–218.

Comments

F. E. J. FRY — Actually, you've almost delivered the last lecture that I've been trying to deliver for some time. I tried some of these ideas in a graduate seminar a few years ago, and some in the audience thought I was nuts. Rosen's various writings render these ideas more explicitly than any place else I've ever found them. Essentially, these ideas exactly point up the difference between autecology and environmental physiology.

Autecology deals with the activities of organisms. These are the emergent properties, the things we basically study at this level of organization. But to analyze these, you must look at the next lower level, or what I would call the next lower "plane of organization." Then it turns out that the proximal cause for these activities is the energy released to bring them about; and this is the reason for the fine distinction between activity and metabolism, metabolism being simply a generalized term for the energy involved.

So in autecology your business is to know the capacity of the organism; how hard the mule can kick. Then, by analyzing the first mule's kick

(and this relieves you from having all mules kick you) you can use proximate analysis to arrive at a generalization which will allow you to either duck the next mule or kick him back, depending on how the analysis indicates you should respond.

If you then go beyond that in your analysis, you are defeating your purpose. The salient principle here is that whatever I know of muscle physiology would not enable me to predict a mule's kick: for this kind of prediction, I have to understand the system at the appropriate emergent level of behavior.

The general definition of a system is that it is a containment or passage of energy. In the long term it is always a passage, although it may be contained for eons as it is, say, in the nuclei of a water molecule. It is energy then, that is contained or channeled through a pattern of form. The fundamental definition of form is a pattern of forces. We don't quite know what energy is, or what mass is, because these are operational definitions. When you get down to ultimates, nothing remains but operational definitions.

So you have to know, for any level of organization, what the emergent property is. For an ecosystem the emergent property, to me, is simply the level to which energy is contained, as potential energy, compared to the energy flux which is impinged upon it and passes through it.

I said it at the time of my earlier lecture, and I'd like to continue saying it, that the great curse of humanity is the opposable thumb. This governs man's attitude of looking at things. It is typified by the small boy who isn't content to run his toy train, he must take it apart. Having taken his toy train apart, he no longer has one. We fall into this nit-picking, this manipulation by tearing things apart, what you call internal analysis, because it is so much a part of our own organization that it is very difficult for us to look at the emergent properties. In the case of the ecosystem it's almost impossible, because we stand inside it anyway. The great boon to humanity was that people were a long time taking molecules apart, because we would never have learned any chemistry if we had started by taking the molecules apart; we would never have learned any physics either. We learned physics because we couldn't take rocks apart too easily, and this is how you learn to look at mass and energy.

So you have to stand off and look at the whole system to understand its properties. This is the great ecological problem, and this is the great autecological problem. People think its too simple just to measure an activity. But this is all observational, rather than analytical. The truth of the matter is that one man's observations are the next man's analysis. You take the properties of a level of organization and use those observations to analyze the next level of organization below it. If you take the properties too many steps down you're being stupid: and you cannot go in the other direction.

I did actually try to collect some of these ideas into a paper. It didn't get very wide circulation: it was in a little mimeographed publication put out by an engineering outfit in Sydney. The point I made there was that in relation to thermal pollution I can only, from autecology, deal with one question. That question concerns the immediate set of circumstances that will bring about the death of an organism, particularly by a temperature change. When I get into the environment where temperature is not having this sledgehammer effect, where there is interaction, I'm in a situation I can no longer predict. If I'm told what that particular situation is, then by the interaction between limiting and controlling factors, I can manage the specific question. But there is no general way of going from autecology to synecology. There is a way of coming back to autecology from synecology, but you cannot go the other way.

One thing I can't understand is why this is not made explicit in the most elementary of textbooks. Another thing I can't understand is why I can't make it explicit so people don't think it is foolish.

H. A. REGIER — To what extent is the whole concept of emergence a necessary consequence of perceiving nature as hierarchical?

F. E. J. FRY — I was going to end up with another remark, that I think there is a spectrum of hierarchies. If you went back to chaos, it would be what I would call a totally noninteractive system. My notion of a relatively noninteractive system is like a greyhound race, where you have a series of tracks laid out, with a mechanical rabbit that can go faster than any one greyhound. The greyhounds compete with each other but essentially, give or take the actions of the track, your prior knowledge of the performance capabilities of the greyhounds pretty well allows you to predict the outcome of the race. This is a system where each individual is on its own, that is, where each subsystem is on its own, and the result depends upon the unalloyed excellence of the subsystems, not upon their hierarchical integration.

At the other extreme, you have the tightly integrated hierarchy. The nearest thing to a complete hierarchy, I think, is a molecule, where the forces are so balanced that the orbits of the electrons

are set and the whole thing is subservient to the integral patterns of forces. An organism is substantially hierarchical, say ninety percent hierarchical, but not entirely so.

Somewhere in between is an ecosystem, for example. The difference is really between the deterministic and the stochastic fractions in the situation. I haven't got this difference completely clear, well, I'm completely muddled, I suppose. But I'm trying to sort this out and it's the one thing that intrigues me these days (that plus plastic greenhouses).

There is another, related, concept which I really gained from Rosen, that hierarchical systems basically arise by chance — and by chance I don't mean by accident: they arise at a certain statistical level of probability from the noninteractive situations I spoke of a moment ago. This gives rise to the sort of principle of uncertainty that applies when you're trying to fit individual species into an ecosystem. Essentially then, I'm saying, and I'm saying it very gently because I'm hoping rather than believing in this case, that the subsystem tends to be more hierarchical than the system of which it is a subset — so that the largest system of all is the most probabilistic.

S. R. KERR — Another dimension of this question, one that particularly puzzles me at the moment, is whether there are qualitative differences in the categories of emergent properties. For example, the hardness of a crystal is an emergent property, as is the active site of an enzyme, and so on; can these all be analyzed in the same way, or are there qualitative differences that cannot be ignored?

F. E. J. FRY —Yes, hardness of a crystal is a physical property; a property of the lattice, of the interaction of atoms. In the same way, the properties of molecules are chemical properties. I don't want to push this too far, but these are planes of organization: there are physical properties, and there are chemical properties, and there are biological properties, and there are probably social properties — and these are different planes of organization.

S. R. KERR — But are these qualitatively different? Do they result from fundamentally different kinds of integration?

F. E. J. FRY — Well, I wouldn't necessarily know whether they were qualitative differences, because I don't really know what a quality is. I rather think that all qualitative differences are quantitative differences in sites and speeds of changes, and I don't know any more about it. They are quantitative differences in complexity of form, to go back to the fundamental definition, being patterns of forces.

S. R. KERR — I wish I understood that.

F. E. J. FRY — I wish I did too, I'd write a paper on it.

L. M. DICKIE — Do you make observations on different scales for each of these planes of organization?

F. E. J. FRY — Oh yes.

L. M. DICKIE — But these kinds of observation themselves aren't different are they? It's the same observer?

F. E. J. FRY — It's the same observer, but he's making a different measurement. You can't measure a chemical property with a meter stick, you can only measure a physical property that way. You can't judge a piece of music that way.

L. M. DICKIE — You can, but you're measuring something irrelevant.

F. E. J. FRY — That's right. I think that is an important difference, that you use a different kind of measuring device for each level of organization, by and large. That may be a first approximation to a reasonable generalization.

L. M. DICKIE — What troubles me in this instance is that I don't know how to cope with the linkages between hierarchical levels. For example, if I talk about the use of food in a system, I'm faced with the problem that at one level I have a population of a certain density, this density affects the amounts that each individual eats, this in turn induces certain rates of enzyme induction in the stomachs of the individuals. Now what seems important here is that there is a population influence on enzyme induction. Am I going down two hierarchical levels in this linking?

F. E. J. FRY — I think you are. The problem here is fundamental to the relation of autecology to physiology and biochemistry.

L. M. DICKIE — It seems to me what I've got to do to know that system is set up an explicit set of observations about density and induction of enzymes, which is not a thing you can do by looking at any individual pair of adjacent hierarchical levels.

S. R. KERR — Rosen has something to say in this context. He talks about, in some sense, the artificialities of our descriptions of systems. He speaks, in a way that I dimly understand, of remapping the true state variables of the system into tractable observables. I think this is essentially the process that you are talking about.

F. E. J. FRY — Well, this is the whole trick. The trick is to look at the levels you're concerned with in a way that will deal with the properties that the system presents you with.

H. A. REGIER — But how can you know at the outset whether or not your perspectives or your preceptions are getting in the way?

F. E. J. FRY — You don't — and of course that's exactly what happens. The whole trick in observation (this was A. G. Huntsman's text throughout his life) is to look at the thing with completely unbiased eyes. And this is a very difficult thing to do.

H. A. REGIER — It's not possible.

F. E. J. FRY — No, it's not possible, therefore you look at the thing from this place and that place, and kick the thing, and poke it here and there. You must have a whole experience before you can get rid of your original bias. You can improve your observations with experience, as well as completely wreck them. This means that you have to work your way into a particular subject.

S. R. KERR — At what stage in your work did these ideas become explicit?

F. E. J. FRY — These ideas? They're not explicit yet. I believe that I was the first to deal with the explicit partitioning of activity and metabolism. I don't think that any of my colleagues or immediate predecessors were working in this direction. In fact, I think that things were clearer in this respect in the work of the 1890s.

I was concerned with the problem about 1946. It was just after the war, and I wasn't teaching that winter. I had done a bit of work on lethal factors, and as a result had come very painfully to the extremely simple generalization of the differences between resistance and tolerance. I'd decided to sort the thing out, and I kept at it for that winter. I didn't quite know what I'd done until the end of that winter, when I came up with the 1947 paper, and basically, I haven't been able to change my thinking very much from that time.

FIG. 1. Participants of the Fry Symposium. A. H. Berst, W. J. Christie, and D. Stevens not included. (Photograph by R. W. McCauley.)

Selected Excerpts from Symposium Discussion Periods

"The hand is the cutting edge of the mind"

Jacob Bronowski/ Ascent of man

"The great curse of humanity is the opposable thumb"

F. E. J. Fry/ this symposium

The program for this Symposium allowed ample opportunity for extended discussion. In particular, the final morning was largely given over to further elaboration of matters raised during the previous 2 days. Because of space limitations, the major part of the substantive discussions cannot be reported here, despite their substantial scientific interest.

Instead, the editor has chosen to use selected extracts from the discussions which further develop the central, unifying theme as it emerged from the proceedings. The considerable illumination shed by Dr Fry upon his fundamental conceptual approach to science came as a welcome surprise to those in attendance, despite the fact that all had enjoyed, in various capacities, considerable prior contact with him. These insights are not available elsewhere, and they reveal much about one of the great men of Canadian science.

A major aspect of the Fry paradigm is embodied in the two quotations which begin this section. As with all good aphorisms, each expresses a pervasive truth, with a compactness exceeding that of mathematical notation. Despite their seeming contradiction, these aphorisms are in fact complementary, and their complementarity is fundamental to the Fry paradigm.

Quite clearly, as stated elsewhere by Rosen, and repeated earlier in this account of the Symposium, there are just two general methods of analysis that are available to science: internal analysis, and external analysis. This is the apparent paradox of the aphorisms. The Fry paradigm, contrary to the fashion in much of current science, (if you doubt this point, examine the achievements of the Nobel laureates in science for the past decade) does not espouse the method of internal analysis as its principal approach. Neither does it reject internal analysis, the rationale of the opposable thumb. Instead it recognizes the serious constraints to which internal analysis is subject, and, as its complement and necessary analytical predecessor, accords external analysis its due importance.

Fry made this view abundantly clear in two general ways throughout the Symposium. In the first, more abstract way he repeatedly emphasized the general definition of form as a pattern of forces, whereby all systems have their energy channeled by coherent form. Form, in these terms, can exist either in space or in time, in the sense that containment of energy can occur within a periodic oscillation in time as much as it can within a spatial pattern.

From this general view, it follows that comprehension of the integral pattern of forces observable at a given level of organization necessarily precedes internal analysis at lower organizational levels. One of the many examples he offered in support of this point is, in his terms,

F. E . J. Fry ... the principle that an animal does what it can, and quits while it's still ahead. This is one of the problems with the metabolic rate/body size equation, and it's also very clear in osmoregulation. One of the oldest observations of this is that the respiratory rate goes down when you place a salt water fish in fresh water. The respiratory rate goes down because the darn fish won't open its mouth. The animal will restrict itself in order to exist.

The second general way in which Fry clarified his conceptual outlook was through his explanation of factors analysis, an important component of his scientific contributions. The following illustrative excerpt reproduces his response to the request, by Henderson, for an explanation of the necessity for masking factors within the Fry system of factors analysis.

Printed in Canada (J4038)
Imprimé au Canada (J4038)

F. E. J. FRY The necessity for having the group is that this is what regulation is all about. At any level of any hierarchical system there has to be some interplay of form and energy which maintains that system. The basis is that energy is channeled through form, and this leads to the persistence of the system. A rapids in a river is a system because the standing wave is always in the same place, essentially. It persists in the same place because of the hydrodynamic equilibria.

N. HENDERSON I'm more troubled than ever!

F. E. J. FRY There really are only two basic factors. These are the controlling factors, the state of activation of matter; and the limiting factors, which is the availability of matter. So you can resolve the whole argument to the interplay of those two factors. The introduction of masking factors comes in as a, to me, very illuminating supplementary category, because it covers the costs of regulation.

The interactions themselves are in the universe. The interactions are available to the organism, they may well be manufactured on the spot, within the organism, with an enzyme. An enzyme is exactly that: an enzyme takes advantage of the conformation of the atoms to produce a property which allows metabolism to go on in the face of the prevailing temperature.

So that is a masking factor. What is taken advantage of is the property of the atomic distances and sequences, which is a pretty abstruse picture. The example I've used almost ad nauseam is the one of sweat to control higher temperatures. The environment is impinging on the organism in terms of solar radiation, and the organism has to dissipate the radiation. To dissipate the radiation, it has developed a system which takes advantage of the latent heat of fusion. These are two environmental properties, radiant energy and latent heat of fusion. The organism has to provide a matrix for that to operate to its own advantage. It isn't powerless.

The other sort of hackneyed illustration that I use is that of a corporation lawyer. You have to abide by the law, but if you can work one law against another one then you can abide. This is what regulation is all about.

L. M. DICKIE Yesterday you said something to the effect that if you go up through the system, through higher and higher levels of organization, you go from determinate form to statistical form. If I understand correctly, you're saying that the cost of the form is equated with masking factors. Now, when you're up in the higher levels, this forage availability factor that we talk about, this q, would you call that a masking factor?

F. E. J. FRY I have difficulty in setting the factors, as described in autecology, into synecology. They fit in some way, but they really fit by working on the individual, so they're not community properties: it's much the same relation as physiology has with autecology. Essentially, hierarchical systems arise from stochastic ones, the odds being weighted by the "factors," as I use the term.

From this, the discussion went on to consider points raised by Brett, and others, as to the generality of these views. In response to the question as to how far this view of factors could be taken (e.g. to temperature, ionic regulation) Fry had this to say:

F. E. J. FRY I would take it to the nth degree, this is the essence of the whole organism. It is all organic regulation.

In short, the view is that regulation can be achieved only through form, and cannot be understood without integral observation of emergent form itself made at the level of organization that is appropriate to the question being asked.

As a parting, epistemological extension of the Fry paradigm, the following exchange may be of interest:

H. A. REGIER Have you ever wondered what you lost by conceptualizing the problem the way you did?

F. E. J. FRY ... What I lost by becoming an autecologist was the ability to become

a synecologist. If I had become a synecologist I'd have lost the ability to become a philosopher. I do believe that the man who can deal with the broadest system of the universe is the top man; he's the man who has the most intellectually satisfying system. If I'd become a chemist, I'd have lost the ability to become a biologist at all. On the other hand, because of the nature of things, and depending on your own human nature, I think you get the greatest satisfaction in handling the level of detail that you can encompass to the greatest degree. The man who understands the universe is a very lonely creature, but within his own mind I think he has the greatest satisfaction.

Acknowledgments

The Symposium could not have been the serendipitous occasion it was, of course, without the enthusiastic involvement of the various participants. Neither could it have begun, much less succeeded, without the substantial assistance of various administrators blessed with the acumen to recognize a good thing: these include (in alphabetical order) K. K. Irizawa, W. R. Martin, and J. D. Roseborough. The principal agencies that supported the undertaking, the Fisheries Research Board of Canada, and the Ontario Ministry of Natural Resources, did so substantially, and in approximately equal part.

Equally essential support was given by D. Cucin, J. Ferrigan, B. Kukhta, J. MacLean, and J. Murdock, among others.

The editors of these proceedings, A. H. Lawrie, and S. R. Kerr, warrant special accolades.

To each of these, and to Dr Fry in particular, our deepest thanks.

K. H. Loftus
H. A. Regier
H. H. Harvey
S. R. Kerr
Organizing committee

Profile of F. E. J. Fry

I. Curriculum Vitae

Fry, Frederick Ernest Joseph

Born: Woking, Surrey, England April 17, 1908
B.A. University of Toronto, 1st Cl.Hon. Biology 1933
M.A., Ph.D. University of Toronto, 1935, 1936
Graduate work in aquatic ecology
Teaching and research interests, ecology with special reference to freshwater organisms. Author of some 60 scientific publications. Cotranslator of "Ruttner — Fundamentals of Limnology"
Research assistant University of Toronto, 1936
Various posts to Professor of Zoology, 1936–56
1941–45 War Service with Royal Canadian Air Force with research responsibilities in aviation medicine
Discharged as Squadron Leader
Awarded M.B.E. 1944
Consultant, Ontario Department of Lands and Forests
U.S. Public Health Service, to 1968
1948 Elected Fellow, Royal Society of Canada
1950 Received citation from Wildlife Society of America for best publication in fisheries biology
1951 President, American Society of Limnology and Oceanography
1955 Visiting Professor, University of Hawaii
1959 Guggenheim Fellow
1962 Recipient of the Flavelle Medal of the Royal Society of Canada for excellence in research
1962 Vice-President, International Association for Pure and Applied Limnology
1964 Member, Fisheries Research Board of Canada
1965 Chairman, Associate Committee on Water Pollution Research, National Research Council of Canada
1965 Member, Board of Consultants on Bay-Delta Project, California Water Quality Control Board
1965 Member, Scientific Advisory Board and Economic Study Group, International Great Lakes Fishery Commission
1966 President, American Fisheries Society
1966 President, Canadian Society of Zoologists
1967 Member, U.S. National Technical Advisory Committee on Water Quality Requirements
1968 Awarded Canada Centennial Medal for "Services to the Nation"
1968 Visiting Professor, University of Hawaii
1969 Commissioner, International Great Lakes Fishery Commission
1970 Awarded honorary degree of D.Sc., University of Manitoba
1971 Awarded Bronze Medal of the American Fisheries Society for outstanding contributions to fisheries science
1972 President, American Institute of Fishery Research Biologists
1973 Consultant in thermobiology to the Argonne National Laboratory
1974 Fry medal established by the Canadian Society of Zoologists, elected honorary member of society
1974 Professor Emeritus University of Toronto
1974 Associate, Institute for Environmental Studies, University of Toronto

II. "In Retirement"

On his retirement from the Department of Zoology, University of Toronto in 1974, Dr Fry was appointed Professor Emeritus. He continues as an Associate with the Institute for Environmental Studies, University of Toronto, on a part-time basis. He is a part-time Consultant to the firm of James F. MacLaren Ltd. who have a contract with the New Brunswick Electric Power Commission at the Lepreau Nuclear Generating Station Project, N.B. He is also the editor of the new *Journal of Great Lakes Research* published by the International Association for Great Lakes Research.

In his spare time (sic) he is an enthusiastic gardener. He hopes that one day he will be able to build a cottage on his land at Manitoulin Island that will be heated principally by solar heat with which he has been experimenting for the last decade.

Of course he still, as always, has an open door where students and associates go to him for advice on their problems and inevitably leave in a much happier frame of mind.

III. List of Dr F. E. J. Fry's Publications

1. Dymond, J. R., and F. E. J. Fry. 1932. Notes on the breeding habits of the green snake (*Liopeltis vernalis*). Copeia 2: 102 p.
2. Fry, F. E. J. 1937. The summer migration of the cisco, *Leucichthys artedi* (Le Sueur) in Lake Nipissing, Ontario. Univ. Toronto Stud. Biol. Ser. 44, Publ. Ont. Fish. Res. Lab. 55:1–91.
3. Fry, F. E. J., and W. A. Kennedy. 1937. Report on the 1936 lake trout investigation, Lake Opeongo, Ontario. Univ. Toronto Stud. Biol. Ser. 42, Publ. Ont. Fish. Res. Lab. 54: 1–120.
4. Fry, F. E. J., E. C. Black, and P. F. Elson. 1937. A note on the effect of the increased carbon dioxide content of water on the buoyancy of the anaesthetized guppy, *Lebistes reticulatus* (Peters). Abstr. Trans. R. Soc. Can. May Meeting: 52 p.
5. Fry, F. E. J., E. C. Black, and L. Irving. 1938. The effect of CO_2 in water upon respiration of fish. Science 88: 502 p.
6. Fry, F. E. J. 1939. A comparative study of Lake trout fisheries in Algonquin Park, Ontario. Univ. Toronto Stud. Biol. Ser. 46, Publ. Ont. Fish. Res. Lab. 58: 1–69.
7. 1939. The position of fish and other higher animals in the economy of lakes. Am. Assoc. Adv. Sci. 10: 132–142.
8. 1939. The influence of carbon dioxide on the utilization of oxygen by certain species of fish in the Toronto region. Am. J. Physiol. 126: 497–498.
9. Fry, F. E. J., J. R. Brett, and G. H. Clawson. 1942. Lethal limits of temperature for young goldfish. Rev. Can. Biol. 1: 50–56.
10. Harkness, W. J. K., and F. E. J. Fry. 1942. Game fish management in Algonquin Park Lakes. Trans. North Am. Wildl. Conf. 7: 398–404.
11. Fry, F. E. J. 1943. A method for the calculation of the growth of fishes from scale measurements. Univ. Toronto Stud. Biol. Ser. 51, Publ. Ont. Fish. Res. Lab. 61: 5–18.
12. Fry, F. E. J., J. S. Hart, and K. F. Walker. 1946. Lethal temperature relations for a sample of young speckled trout (*Salvelinus fontinalis*). Univ. Toronto Stud. Biol. Ser. 54, Publ. Ont. Fish. Res. Lab. 66: 1–47.
13. Cuerrier, J. P., F. E. J. Fry, and G. Prefontaine. 1946. Liste preliminaire des poissons de la region de Montreal et du Lac Saint-Pierre. Nat. Can. 73: 17–32.
14. Fry, F. E. J., V. S. Black, and Edgar C. Black. 1947. Influence of temperature on the asphyxiation of young goldfish (*Carassius auratus* L.) under various tensions of oxygen and carbon dioxide. Biol. Bull. 92: 217–224.

15. FRY, F. E. J. 1947. The South Bay experiment. Sylva 3: 15–25.
16. 1947. Effects of the environment on animal activity. Univ. Toronto Stud. Biol. Ser. 55, Publ. Ont. Fish. Res. Lab. 68: 1–62.
17. FRY, F. E. J., AND J. S. HART. 1948. The relation of temperature to oxygen consumption in the goldfish. Biol. Bull. 94: 66–67.
18. FRY, F. E. J., AND V. . CHAPMAN. 1948. The lake trout fishery in Algonquin Park from 1936 to 1945. Trans. Am. Fish. Soc. 75: 19–35.
19. FRY, F. E. J., AND J. S. HART. 1948. Cruising speed of goldfish in relation to water temperature. J. Fish. Res. Board Can. 7: 169–175.
20. FRY. F. E. J. 1949. Lake trout in our inland waters. Sylva 5:3–13.
21. FRY, F. E. J., A. C. BURTON, AND O. G. EDHOLM. 1949. A simple gas analyser. Can. J. Res. 27: 188–194.
22. FRY, F. E. J. 1949. Statistics of a lake trout fishery. Biometrics 5: 27–67.
23. 1950. A splashless tank for transporting fish. Can. Fish Cult. 10: 1–2.
24. 1951. Some temperature relations of fish. Fed. Proc., Am. Soc. Exp. Biol. 10: 46 p.
25. 1951. Some environment relations of the speckled trout (*Salvelinus fontinalis*). Proc. Northeast. Atl. Fish. Conf. p. 1–29.
26. 1951. A fractionating column to provide water of various dissolved oxygen content. Can. J. Technol. 29: 144–146.
27. 1952. The role of research in fisheries management in Ontario from the research point of view. Can. Fish Cult. 12: 20–21.
28. RUTTNER, F. 1952. Fundamentals of limnology. (Translated by F. E. J. Fry and D. G. Frey) University of Toronto Press, Toronto, Ont. p. 1–108.
29. FRY, F. E. J. 1953. The 1949 year class of lake trout in south Bay, Lake Huron. Trans. Am. Fish. Soc. 82: 178–192.
30. FRY, F. E. J., AND M. B. GIBSON. 1953. Lethal temperature experiments with speckled trout × lake trout hybrids. J. Hered. 44: 56–57.
31. GIBSON, E. S., and F. E. J. FRY. 1954. The performance of the lake trout, *Salvelinus namaycush*, at various levels of temperature and oxygen pressure. Can. J. Zool. 32: 252–260.
32. BLACK, E. C., F. E. J. FRY, AND V. S. BLACK. 1954. The influence of carbon dioxide on the utilization of oxygen by some freshwater fish. Can. J. Zool. 32: 408–420.
33. FRY, F. E. J. 1956. Movements of drift cards in Georgian Bay in 1953. J. Fish. Res. Board Can. 13: 1–5.
34. FRY, F. E. J., and K. E. F. WATT. 1957. Yields of year classes of the smallmouth bass hatched in the decade of 1940 in Manitoulin Island waters. Trans. Am. Fish. Soc. 85: 136–143.
35. FRY, F. E. J. 1957. The aquatic respiration of fish, p. 1–63. *In* M. E. Brown [ed.] The physiology of fishes I. Academic Press, Inc., New York, N.Y.
36. 1957. The lethal temperature as a tool in taxonomy. Annee Biol. 33: 205–219.
37. 1958. Temperature compensation. Annu. Rev. Physiol. 20: 207–224.
38. FRY, F. E. J., AND J. C. BUDD. 1958. The survival of yearling lake trout planted in South Bay, Lake Huron. Can. Fish Cult. 23: 1–9.
39. GARSIDE, E. T., and F. E. J. FRY. 1959. A possible relationship between yolk size and differentiation in trout embryos. Can. J. Zool. 37: 383–386.
40. FRY, F. E. J. 1959. The oxygen requirements of fish. U.S. Public Health Serv., R. A. Taft, Sanit. Eng. Cent., Tech. Dep. W60-3: 106–109.
41. 1960. Requirements for the aquatic habitat. Pulp Paper Mag. Can. Tech. Sect., Feb.: 3–8.
42. BUDD, J. C., AND F. E. J. FRY. 1960. Further observations on the survival of yearling lake trout planted in South Bay, Lake Huron. Can. Fish Cult. 26: 7–13.
43. FRY, F. E. J., D. CUCIN, J. C. KENNEDY, and A. PAPSON. 1960. The use of lead versenate to place a time mark on fish scales. Trans. Am. Fish. Soc. 89: 149–153.

44. McCombie, A. M., and F. E. J. Fry. 1960. Selectivity of gill nets for lake whitefish, *Coregonus clupeaformis*. Trans. Am. Fish. Soc. 89: 176–184.
45. Fry, F. E. J., and K. S. Norris. 1962. The transportation of live fish, p. 595–608. *In* G. Borgstrom [ed.] Fish as food. Academic Press, Inc., New York and London.
46. Fry, F. E. J., and V. Legendre. 1963. Ontario and Quebec, p. 487–519. *In* D. G. Frey [ed.] Limnology in North America. Wisconsin University Press, Madison, Wis.
47. Arai, M. N., E. T. Cox, and F. E. J. Fry. 1963. An effect of dilutions of seawater on the lethal temperature of the guppy. Can. J. Zool. 41: 1011–1015.
48. Fry, F. E. J. 1964. Animals in aquatic environments: fishes, p. 715–728. *In* D. B. Dill [ed.] Handbook of physiology. 4: adaptation to the environment. Am. Physiol. Soc., Washington.
49. ———— 1967. Responses of vertebrate poikilotherms to temperature, p. 375–409. *In* A. H. Rose [ed.] Thermobiology. Academic Press, Inc., London.
50. Anderson, D. V., and F. E. J. Fry. 1967. The thermal regime of Georgian Bay (1953, 1954). Ont. Dep. Lands For. Res. Rep. 80: 32 p.
51. Budd, J. C., F. E. J. Fry, and J. B. Smith. 1968. Survival of marked lake trout in Lake Manitou, Manitoulin Island, Ontario. J. Fish. Res. Board Can.. 25: 2257–2268.
52. Budd, J. C., F. E. J. Fry, and P. S. M. Pearlstone. 1969. Final observations on the survival of planted lake trout in South Bay, Lake Huron. J. Fish. Res. Board Can. 26: 2413–2424.
53. Fry, F. E. J. 1969. Some possible physiological stresses induced by eutrophication, p. 531–536. *In* Eutrophication: causes, consequences, correctives. Nat. Acad. Sci., Washington, D.C.
54. Stevens, E. D., and F. E. J. Fry. 1970. The rate of thermal exchange in a teleost, *Tilapia mossambica*. Can. J. Zool. 48: 221–226.
55. Fry, F. E. J., and P. W. Hochachka. 1970. Fish, p. 79–134. *In* G. C. Whittow [ed.] Comparative physiology of thermoregulation. Vol. 1. Academic Press, Inc., New York, N.Y.
56. Fry, F. E. J., and E. T. Cox. 1970. A relation of size to swimming speed in rainbow trout. J. Fish. Res. Board Can. 27: 976–978.
57. Stevens, E. D., and F. E. J. Fry. 1971. Brain and muscle temperatures in ocean caught and captive skipjack tuna. Comp. Biochem. Physiol. 38: 203–211.
58. Fry, F. E. J. 1971. The effect of environmental factors on the physiology of fish, p. 1–98. *In* W. S. Hoar and D. J. Randall [ed.] Fish physiology. Vol. VI. Academic Press, New York, N.Y.
59. Martin, N. V., and F. E. J. Fry. 1972. Lake Opeongo: Effects of exploitation and introductions on the salmonid community. J. Fish. Res. Board Can. 29: 795–805.
60. Stevens, E. D., and F. E. J. Fry. 1972. The effect of changes in ambient temperature on spontaneous activity in skipjack tuna. Comp. Biochem. Physiol. 42: 803–805.
61. Fry, F. E. J. 1972. Thermal facilitation and thermal stress, p. 5–19. *In* Thermal discharge engineering and ecology. Thermo-Fluids conference, Dec. 4–7, 1972. Inst. Eng., Sydney, Australia.
62. Martin, N. V., and F. E. J. Fry. 1973. Lake Opeongo. The ecology of the fish community and of man's effect on it. Great Lakes Fish. Comm. Tech. Rep. 24: 34 p.
63. Fry, F. E. J. 1973. Book review of: Biological aspects of thermal pollution by P. A. Krenkel and F. L. Parker [ed.] 1969. Vanderbilt University Press, Nashville, Tenn. 407 p. Can. Field Nat. 87: 205.
64. Stevens, E. D., and F. E. J. Fry. 1974. Heat transfer and body temperatures in non-regulatory teleosts. Can. J. Zool. 1137–1143.

IV. Graduate Students of F. E. J. Fry

Alderdice, D. F.
*Ayles, G. B.
Armstrong, J. J.
Basu, S. P.
Beamish, F. W. H.
Brograd, L.
Brett, J. R.
Coble, D. W.
Craigie, D. E.
Evans, D. O.
Everest, G. L.
Fahmy, F. K.
Ferguson, R. G.
Fraser, J. M.
Garside, E. T.
Gibson, M. B.
Graham, J. J.
Graham, J. M.
Griffiths, J. S.
Hallam, J. C.
Hart, J. S.
Henderson, N. E.
**Hurley, G. V.
Ihssen, P. O. E.
Job, S. V.
Kennedy, W. A.
Kutty, M. N.
***Lawler, G. H.
Lin, E. C.
K. H. Loftus
Martin, N. V.
Martin, W. R.
McCauley, R. W.
***McCracken, F. D.
Meth, F. F.
Muir, B. S.
Neil, J. H.
Payne, N. R.
Rao, G. M. M.
Sale, P. F.
Saunders, R. L.
Shepard, M. P.
Spangler, G. R.
Tait, J. S.
Tyler, A. V.
Wainio, A.
White, W. J.

*with Dr L. Butler
**with Dr H. A. Regier
***after J. R. Dymond

LIST OF PARTICIPANTS

Dr D. F. Alderdice
Department of the Environment
Nanaimo, British Columbia

Mr A. H. Berst
Ministry of Natural Resources
Maple, Ontario

Dr J. R. Brett
Department of the Environment
Nanaimo, British Columbia

Mr W. J. Christie
Ministry of Natural Resources
Glenora, Ontario

Mr D. Cucin
Ministry of Natural Resources
Maple, Ontario

Dr L. M. Dickie
Dalhousie University
Halifax, Nova Scotia

Dr D. Evans
University of Toronto
Toronto, Ontario

Mr J. M. Fraser
Ministry of Natural Resources
Maple, Ontario

Dr F. E. J. Fry
University of Toronto
Toronto, Ontario

Dr S. Griffith
University of Toronto
Toronto, Ontario

Dr J. C. Hallam
Ontario Science Centre
Toronto, Ontario

Dr H. H. Harvey
University of Toronto
Toronto, Ontario

Dr N. E. Henderson
University of Calgary
Calgary, Alberta

Dr P. Ihssen
Ministry of Natural Resources
Maple, Ontario

Mr K. K. Irizawa
Ministry of Natural Resources
Toronto, Ontario

Dr S. R. Kerr
Ministry of Natural Resources
Maple, Ontario

Mr A. H. Lawrie
Ministry of Natural Resources
Maple, Ontario

Mr K. H. Loftus
Ministry of Natural Resources
Toronto, Ontario

Dr R. W. McCauley
Wilfred Laurier University
Waterloo, Ontario

Dr J. MacLean
Ministry of Natural Resources
Maple, Ontario

Mr N. V. Martin
Ministry of Natural Resources
Maple, Ontario

Dr W. R. Martin
Department of the Environment
Hull, Quebec

Dr B. S. Muir
Department of the Environment
Dartmouth, Nova Scotia

Dr H. A. Regier
University of Toronto
Toronto, Ontario

Mr J. D. Roseborough
Ministry of Natural Resources
Maple, Ontario

Mr R. A. Ryder
Ministry of Natural Resources
Thunder Bay, Ontario

Dr R. L. Saunders
Department of the Environment
St. Andrews, New Brunswick

Dr G. R. Spangler
Ministry of Natural Resources
South Baymouth, Ontario

Dr J. B. Sprague
University of Guelph
Guelph, Ontario

Dr W. M. Sprules
Ottawa, Ontario

Dr D. Stevens
University of Hawaii
Honolulu, Hawaii

Dr J. S. Tait
York University
Downsview, Ontario

Dr A. V. Tyler
Oregon State University
Newport, Oregon

BOOK REVIEWS/COMPTES RENDUS

Marine Science Communications — Basic and Applied. *D. W. Hood ed. Vol. 1. Published bimonthly by Marcel Dekker, Inc., New York, N.Y. 1975. Subscription rate for Vol. 1, $35.00 + $6.50 postage outside USA. ii + 100 p.*

This is another of a rash of "Letters," or in this case, "Communications," now appearing for quick publication of papers. One takes a hasty glance through such a periodical and is somewhat taken aback initially by the double-spaced, typewritten pages reduced presumably photographically to a more conventional size than the 8½ × 11 paper on which the material is typed. The question one immediately poses is whether reliable material is being published in a medium which sacrifices the normal refereeing and editorial process in the interest of speed of issue (reputedly 12–16 weeks after receipt of manuscript).

These types of journals rely heavily on the wisdom of the editors to cull the submissions and avoid publication of fraudulent material. So we look at the editorial roster and the list of names in the International Editorial Advisory Boards (one deals with the Basic Research Section and the other with the Applied Research Section), and examine the credentials of individuals involved. It so happens that I know the Editor, Dr Donald Hood quite well personally, and have considerable respect for his abilities in the marine field (formerly at Texas A & M and now Director of the Institute of Marine Science at the University of Alaska) and as an editor of at least two volumes on marine topics, particularly, a recent work on the impact of man on the ocean environment. There are some distinguished names on the advisory boards, which read almost like an international Who's Who in the Marine Sciences, e.g. Sigeru Motoda of Japan, John Steele of Scotland, Michael Mullin of the USA, J. D. Burton of the UK, Olga Koblentz-Mishke of the USSR, George Pickard of Canada, Ernst Føyn of Norway, and Hiroshi Kasahara of the FAO in Rome. Let us hope that the editor and his associate editors make use of these people to properly review submissions relevant to their particular areas of expertise. One might find that the list of editors and advisory board members is rather heavily biased to the University of Alaska, with 5 Alaskans out of a total of 44 names. However, the editor might be forgiven for "stacking" the boards with local colleagues, inasmuch as expediency of the review process in being able to turn to an authority in an adjoining office or laboratory more than compensates for the uneven geographical distribution of advisers.

What does the first issue of Marine Science Communications have to offer? Well, besides the Editorial by Dr Hood, it has six papers, five of which are coauthored by members of the two advisory boards. This is not an unusual way for launching a new journal. No doubt, as it gets better known by members of the marine science community, there will be more "outsiders" contributing. The format of the papers is quite conventional, and the reader should have no difficulty in following the text from Introduction, through Results and Discussion. Each paper begins with a concise, informative Abstract and ends with References, given in the normal fashion for biological journals, with title spelled out in full. The figures were neatly prepared and clearly legible in all papers of this first issue. At the end of each paper, the name of the reviewer is cited, so that there is no anonymity in the review process, as usually practised in traditional refereed journals.

The editors are striving to achieve a good blend of basic and applied papers in the marine sciences. This issue had comparatively basic papers on: 1) nutrient regeneration by oceanic zooplankton: a comparison of methods; 2) association of mercuric ions and humic acid in sodium chloride solution; 3) large-scale ocean and atmospheric patterns relative to the 1957–58 temperature anomaly in the North Pacific Ocean; and 4) plutonium observed on algal surfaces in the ocean. The more applied and longer papers were on concrete in the oceans, and water composition and biogeochemical gradients in the Canton Atoll Lagoon.

I would conclude that this type of journal has a place in the marine sciences, considering the amount of new material in ocean studies that is becoming available every year. It is essential that the information be disseminated rapidly, if we are to advance without unnecessary duplication, and the new knowledge is to be made available to users the world over. Technical reports, with rather limited distribution, hardly meet this need. If it is properly managed, *Marine Science Communications* should flourish and have appeal to a broad segment of the marine science community.

M. WALDICHUK

Department of the Environment
Fisheries and Marine Service
Pacific Environment Institute
West Vancouver, B.C. V7V 1N6

(R86)

Books Received/Livres reçus

August–October 1975

Coastal Zone: Framework for Management in Atlantic Canada. *By Douglas M. Johnston, A. Paul Pross, and Ian McDougall, with the special assistance of Norman G. Dale. Institute of Public Affairs, Dalhousie University, Halifax, N.S. 1975. xiii + 201 p, with a 45-p. appendix. $10.00.*
(Report of a study to examine the need for new initiatives in coastal zone management; contains positive recommendations for introduction of improvements in Atlantic Canada.)

The European Freshwater Eel. *V. R. Sinha and J. W. Jones. Liverpool University Press, Liverpool. 1975. xv + 146 p. £6, about $14.40 Canadian.*
(Covers the eel's life cycle, spawning, distribution, growth, food intake, age estimation, and methods of catching.)

Heavy Metals in the Aquatic Environment. Supplement to Progress in Water Technology. Proceedings of the International Conference held in Nashville, Tennessee, December 1973. *Pergamon Press, Oxford. 1975. x + 352 p. £21, $50.00 U.S.*
(Includes sessions on toxicology and physiology, analytical techniques, transport mechanisms, distribution of heavy metals in the environment, source reduction methodology, corrective measures for existing problems, and legislation, standards surveillance, and monitoring.)

Invertebrates of Southern California Coastal Waters. I. Select Groups of Annelids, Arthropods, Echinoderms, and Molluscs. *Edited by Jack Q. Word and Danuta K. Charwat. Southern California Coastal Water Research Project, El Segundo, Calif. 1975. v + 164 p. $6.00.*
(First volume in a planned series, derived from a taxonomic standardization program to provide uniformity of identification by biologists in southern Cailfornia; focuses on organisms at depths to 200 m in trawl, grab, or dredge samples.)

Limnology. *Robert G. Wetzel. W. B. Saunders Company, Philadelphia, London, Toronto, Ont. 1975. xii + 743 p. $18.05.*
(Summary text for undergraduates; treats distribution, origins, and forms of lakes, water economy, light in lakes, fate of heat, water movements, oxygen, salinity of inland waters, inorganic carbon, N, Fe, E, Si cycles, phytoplankton, zooplankton–benthic fauna–fish community interactions, organic carbon cycle and detritus, littoral zone, and ontology and evolution of lake ecosystsms.)

Proceedings of the Fort Union Coal Field Symposium. *Sponsored by the Montana Academy of Sciences at Eastern Montana College, Billings, Mont., April 1975. vi + 706 p. $8.75 for packaged five volumes available prepaid from Eastern Montana College Bookstore, Billings, Mont. 59101, U.S.A.*
(Volume I includes table of contents for all five volumes, cross-referenced index, and papers of the general session and Administration Section; Volume II, Aquatic Ecosystems Section; Volume III, Reclamation Section; Volume IV, Social Impact Section; and Volume V, Terrestrial Ecosystems Section).

Water Resources of the World. Selected Statistics. *Frits van der Leeden. Water Information Center, Inc., Port Washington, N.Y. 1975. xi + 568 p. $32.50.*
(Data for 138 countries and territories for stream flow and runoff, ground water, water use, irrigation, industrial and public water requirements, and water use projections. Also covers worldwide data on climates, oceans, the hydrologic cycle, characteristics of major rivers, lakes, reservoirs, and dams, availability of hydrologic information, water supply in developing nations, desalination, and financing of water projects by international organizations.)

COMING NEXT MONTH / À PARAÎTRE LE MOIS PROCHAIN

Editor's Foreword/Note du directeur — **J. C. Stevenson**
Preface/Préface — **N. M. Burns**
Lake Erie and its basin — **P. G. Sly**
Continuous dynamical computations of water transports in Lake Erie for 1970 — **T. J. Simons**
Surficial sediments of Lake Erie — **R. L. Thomas, J.-M. Jaquet, A. L. W. Kemp, and C. F. M. Lewis**
Mercury in the surficial sediments of Lake Erie — **R. L. Thomas and J.-M. Jaquet**
Forms of phosphorus in the surficial sediments of Lake Erie — **J. D. H. Williams, J.-M. Jaquet, and R. L. Thomas**
Rates of accumulation of phosphorus forms in Lake Erie sediments — **J. D. H. Williams, T. P. Murphy, and T. Mayer**
Cultural impact on the geochemistry of sediments in Lake Erie — **A. L. W. Kemp, R. L. Thomas, C. I. Dell, and J.-M. Jaquet**
Forms of iron and manganese in Lake Erie waters — **N. M. Burns and J. O. Nriagu**
Sediment yields and nutrient loadings from Canadian watersheds tributary to Lake Erie: an overview — **E. D. Ongley**
Temperature, oxygen, and nutrient distribution patterns in Lake Erie in 1970 — **N. M. Burns**
Oxygen depletion in the Central and Eastern basins of Lake Erie, 1970 — **N. M. Burns**
Nutrient budgets for Lake Erie, 1970 — **N. M. Burns**
Numerical computations of advective and diffusive transports of chloride in Lake Erie in 1970 — **D. C. L. Lam and T. J. Simons**
Computations of physical transport and regeneration of phosphorus in Lake Erie, fall 1970 — **D. C. L. Lam and J.-M. Jaquet**
Phosphorus budget for Lake Erie — **N. M. Burns, J. D. H. Williams, J.-M. Jaquet, A. L. W. Kemp, and D. C. L. Lam**
Bacterial distributions in Lake Erie (1967, 1970) — **S. S. Rao and N. M. Burnison**
Lakewide study of phytoplankton biomass and its species composition in Lake Erie, April–December, 1970 — **M. Munawar and I. F. Munawar**
Relationships of phytoplankton biomass with soluble nutrients, primary production, and chlorophyll *a* in Lake Erie, 1970 — **M. Munawar and N. M. Burns**
Seasonal distribution and abundance of crustacean zooplankton in Lake Erie in 1970 — **N. H. F. Watson**
The fish community in Lake Erie — **J. H. Leach and S. J. Nepszy**
Processes within Lake Erie — **N. M. Burns, J.-M. Jaquet, A. L. W. Kemp, D. C. L. Lam, J. H. Leach, M. Munawar, T. J. Simons, P. G. Sly, R. L. Thomas, N. H. F. Watson, and J. D. H. Williams**

Journal of the Fisheries Research Board of Canada

Guide for Authors

A more detailed guide on preparation of manuscripts from theses is available from the Office of the Editor.

Content

We invite submission of manuscripts in the broad field of fisheries management, ocean science, and aquatic environments relative to Canada.

Articles: Reports of research studies of broad scope that are original contributions to science.

Notes: Differ from papers on the basis of scope or completeness, rather than quality of research. They may be on problems with narrow, readily defined limits; on work that is largely confirmatory; on methodology or research techniques; on advances in knowledge arising as by-products of broader studies; on progress in projects that were discontinued; or on preliminary findings that warrant publication before problems are resolved. They may be organized with as much flexibility as articles except that they have no centered headings and should occupy no more than four printed pages.

Reviews: Detailed articles that are critical appraisals of broad areas of investigation, particularly in fields that have shown rapid development in recent years.

Perspectives: Essays of opinion or hypothesis on fisheries, ocean science, aquatic environments, or related topics that are of concern to the professional and layman. References are desirable; informal style is welcomed.

Letters: Opinion on topics recently under discussion in the *Journal*; preferred maximum length, 500 words. The Editor reserves the right to shorten letters and to make other changes to accord with the style of the *Journal*.

Editorial Practices

The *Style Manual for Biological Journals* (3rd ed. American Institute of Biological Sciences, 3900 Wisconsin Ave. NW., Washington, D.C.) is used as the authority in matters of form. The standards for spelling are: *Webster's Third New International Dictionary* and *le Grand Larousse Encyclopédique*. Titles of periodicals are abbreviated as in the *Biological Abstracts* list. References to literature are made by the name-and-year system. The *Journal* follows the names and spelling recommended in *A List of Common and Scientific Names of Fishes from the United States and Canada* (3rd ed. 1970) Special Publication No. 6 of the American Fisheries Society.

Series titles should be avoided. An *abstract* is required for all manuscripts, and should state concisely, in less than 250 words, what was done, the essentials of the new knowledge, and the main conclusions. Abstracts are published in English and French; those submitted in one language only are translated by the *Journal*.

The Editor normally submits each manuscript to at least two *referees*. Contributors are encouraged to suggest at least four names to be added to the list from which referees may be selected.

Illustrations should be submitted as photographic reproductions no larger than a standard page and must accompany the manuscript. Prints should not be mounted, stapled, or clipped. Symbols, letters, and numerals must be neat, and at least 1.5 mm high when the illustration is reduced to the appropriate size. Drawings should, when possible, be grouped to facilitate comparisons.

Proofs are sent to the author, who is responsible for correcting only errors in typesetting. *Alterations to the content must be avoided.*

Fifty *reprints* are supplied free. Additional reprints may be purchased at the time of publication (an order form is sent out with the galley proof). All orders should be sent to the Printing Department, University of Toronto Press, 5201 Dufferin Street, Downsview, Ont. M3H 5T8. Invoices relating to the reprints will be sent out by the Printer. A charge of $40.00 per page is made for articles published. When submitting a manuscript, an author should state that his institution will accept this charge.

Checklist on Manuscripts

Attention to the following questions will expedite appraisal of manuscripts by referees and editors.

Are the findings, interpretations, and conclusions adequately documented and relevant to the purpose of the study?

Are all the tables and figures needed, and organized to facilitate comparisons? Are there inconsistencies between tables or figures and the text, or within the text? Should some of the data be made available separately, in a manuscript report or at a data repository? If you use statistical analysis are the statistics subordinate to the research?

Would any of the text be clearer if condensed? Are summary statements given at the beginning of sections and paragraphs, and are details in sections and paragraphs relevant to their topics? Does the organization of the manuscript follow logically from the statement of purpose in the introduction?

Does the *title* encompass the content of the report?

Does the *abstract* give the essentials of the new knowledge?

Is the *introduction* largely limited to the scope, purpose, and rationale of the study? Is review of the literature limited to defining the problem?

Are details of *materials and methods* limited to what scientists need in understanding the design of the study and in judging adequacy of the data?

Are generalizations on the *results* adequate? Are findings distinguished from inferences from them?

Is *discussion* limited to interpretation and significance of the findings?

Journal de l'office des recherches sur les pêcheries du Canada

Guide des Auteurs

On peut se procurer au bureau du Directeur de la publication un guide plus détaillé pour la préparation de manuscrits à partir de thèses.

Sujets

Nous désirons reçevoir des manuscrits s'insérant dans le vaste domaine de la gestion des pêches, des sciences de la mer et des milieux aquatiques au Canada.

Articles: Comptes rendus d'études d'une portée générale, constituant des contributions inédites à la science.

Notes: Se distinguent des articles par la portée et le degré d'achèvement plutôt que par la qualité des recherches. Elles peuvent traiter de problèmes particuliers et bien définis; de travaux qui sont en grande partie confirmatoires; de méthodologie ou de techniques de recherche; de progrès de la connaissance découlant d'études plus vastes; de développements dans des projets abandonnés; ou de découvertes préliminaires qui méritent d'être publiées avant la solution de problèmes à l'étude. Les notes peuvent être présentées d'une façon aussi souple que les articles, mais elles ne doivent pas porter d'en-têtes centrés ni occuper plus de quatre pages.

Critiques: Articles détaillés constituant une appréciation critique de vastes champs de recherches, particulièrement dans les domaines ayant connu de rapides progrès au cours des dernières années.

Perspectives: Essais de l'opinion ou de l'hypothèse sur les pêches, les sciences de la mer, les milieux aquatiques, ou sur des sujets connexes qui intéressent professionnels et profanes. Il est préférable de donner des références et d'écrire, si possible, dans un style simple.

Lettres: Opinions sur des sujets exposés dans le *Journal*. Longueur maximale préférable: 500 mots. Le directeur se réserve le droit de raccourcir les lettres et de faire d'autres modifications dans le style du *Journal*.

Dispositions générales

Le *Style Manual for Biological Journals* (3e éd., publié par l'American Institute of Biological Sciences, 3900 avenue Wisconsin N.O., Washington, D.C.) sert de guide quant à la forme de présentation. Le *Webster's Third New International Dictionary* et le *Grand Larousse Encyclopédique* font autorité pour l'orthographe des mots. Les titres de périodiques sont abrégés suivant les *Biological Abstracts*. Les références bibliographiques dans le texte doivent suivre le système nom de l'auteur-année. Pour les noms de poissons et leur orthographe, le *Journal* suit les recommandations contenues dans *A List of Common and Scientific Names of Fishes from the United States and Canada* (Troisième édition, 1970), Publication spéciale No. 6 de l'American Fisheries Society.

Il faut éviter les *articles en série*. Un *résumé* doit accompagner chaque texte et doit exposer brièvement (moins de 250 mots) le travail accompli, les points essentiels des connaissances acquises et les principales conclusions. Les résumés paraissent en anglais et en français, le *Journal* veillant à la traduction dans le cas des présentations unilingues.

Le directeur soumet d'ordinaire chaque texte à l'approbation de deux *arbitres* ou plus. Nous encourageons les collaborateurs à suggérer au moins quatre personnes dont les noms pourraient figurer sur la liste des arbitres.

Les *illustrations* doivent être sous forme de reproductions photographiques ne pas dépasser les dimensions d'une page normale et accompagner le texte. Elles ne doivent pas être montées, coupées ni brochées. Les symboles, lettres ou chiffres doivent se détacher avec précision et avoir au moins 1,5 mm de hauter lorsque l'illustration est réduite à la grandeur voulue. Les dessins doivent, autant que possible, être groupés pour faciliter l'étude comparative.

L'auteur doit revoir les *épreuves* qu'on lui remet et en corriger seulement les erreurs typographiques. *Il doit éviter de changer le contenu du texte.*

Cinquante *tirés à part* sont fournis gratuitement. Les tirés à part peuvent être achetés au moment de la publication. Un bon de commande à cet effet accompagne les épreuves; il doit être retourné en même temps que celles-ci, non pas au bureau de la rédaction, mais au Printing Department, University of Toronto Press, 5201 Dufferin Street, Downsview, Ont. M3H 5T8, qui se chargera de la facturer. Les frais sont de $40.00 par page pour la publication des articles. Quand un auteur soumet un manuscrit, il doit spécifier que son institution accepte les frais.

Listes de contrôles pour manuscrits

Une attention particulière aux questions suivantes facilitera l'évaluation des manuscrits par les arbitres et les éditeurs.

Les découvertes, interprétations et conclusions sont-elles bien documentées et pertinentes au but de l'étude?

Les tableaux et figures sont-ils tous nécessaires et agencés pour faciliter les comparaisons? Y a-t-il contradiction entre les tableaux ou les figures et le texte, ou dans le texte même? Est-ce que certaines données devraient être présentées séparément, dans un rapport manuscrit ou dans un dépôt de données? Si vous faites une analyse statistique, la statistique cède-t-elle le pas à la biologie?

Le texte y gagnerait-il en clarté s'il était plus condensé, en tout ou en partie? Contient-il des exposés sommaires au début de chaque section ou paragraphe, et les détails de ces sections et paragraphs son-ils pertinents au sujet traité? La marche du manuscrit est-elle conforme à la logique énoncée dans l'introduction?

Le *titre* est-il concis, tout en étant représentatif du contenu du rapport?

Le *résumé* donne-t-il l'essentiel des connaissances nouvelles?

L'*introduction* se limite-t-elle à une esquisse de la portée, du but et des raisons de l'étude? La revue de la littérature se limite-t-elle à la définition du problème?

La section *matériel et méthode* contient-elle le minimum de détails qui permettront aux autres scientifiques de saisir les grandes lignes de l'étude et de juger de la valeur des données?

Les généralisations sur les *résultats* sont-elles adéquates? Permettent-elles de distinguer entre constatations et déductions?

La *discussion* est-elle limitée à l'interprétation et à l'évaluation des découvertes?

Journal of the Fisheries Research Board of Canada

Guide for Typists Preparing Copy

Read "Guide for Authors" in the current volume of the *Journal*. When in doubt about how to type or arrange details, follow *Journal* practice.

Type the manuscript on white bond paper, not flimsy, preferably size 21.5 × 28 cm (8.5 × 11 inches). If possible, use paper with the lines numbered in the margin. Leave all margins at least 2.5 cm wide.

Double-space all parts of the manuscript, including tables, captions for illustrations, footnotes, and the reference list. Underline only material that is to be printed in italics. Indent the first line of each paragraph in the text and of each footnote.

In titles and headings, capitalize the first letter of each word. For small capitals, use small letters.

Indicate all text footnotes by superscript arabic numerals. Number them consecutively throughout the manuscript, starting with those on the title page. Place each footnote immediately below the reference to it, separating it from the text by horizontal lines.

On the first page type only the title, the authors' names and affiliations, related footnotes, and the running head (see Appendix A). Type the abstract on a separate page (see Appendix B). Number all pages, beginning with the title page and including those for tables and captions for illustrations.

Have the author check the finished manuscript, and send the ribbon copy and two other clear copies to the Office of the Editor.

Tables: Examine the current volume of the *Journal* to see how tables are set up (see Appendix C).
Note especially the following concerning *numbered tables:*

Type each on a separate page, using paper without the lines numbered.

Number them with arabic numerals.

Use horizontal lines above and below the headings and below the columns, and seldom elsewhere. Never use vertical lines; leave extra spaces instead.

Indicate table footnotes by superscript small letters and type them below the table.

Place the tables after the list of references.

Where each table is first referred to, type in the margin "Table — near here."

Note that *text tables* are not numbered, are typed with the text, and seldom need horizontal lines (see Appendix C).

Illustrations: Send a photographic reproduction (no larger than 21.5 × 28 cm) of each illustration with the manuscript. Type the author's name and figure number on a strip of paper and fasten it to the back of the print. Do not write or type on the print itself. Also, type the captions in succession on a separate page, headed "Captions for illustrations." Put this page at the end of the manuscript.

Where each figure is first referred to, type in the margin "Fig. — near here."

Mathematical Expressions, Equations, and Formulas: Leave three spaces above and below lines that have much material in superscripts, and above and below equations and formulas. In the various expressions, place each component in its correct position (see Appendix D).

Show all symbols clearly. In the margin, spell out Greek letters the first time they occur, and distinguish between the small letter *l* and the numeral *one*, and between the capital letter *O* and the numeral *zero*. Make other explanatory notes similarly.

References: Check the text to see that all references in the list are referred to. Type the reference list, double-spaced, in the style used in the *Journal* (see Appendix E). Names of journals are abbreviated as in the *Biological Abstracts* list; if an abbreviation is in doubt, type the name in full.

Spellings: About 100 words common in fisheries journals are listed in Appendix F.

Appendices: Appendices A to F are available on request from the Office of the Editor.

Journal de l'office des recherches sur les pêcheries du Canada

Guide pour les secrétaires d'auteurs

Lisez le "Guide des Auteurs" reproduit dans l'édition courante du *Journal*. Si vous avez des doutes sur la façon de dactylographier le texte ou d'en agencer les détails, suivez la pratique du *Journal*.

Dactylographiez le manuscrit sur papier blanc de bonne qualité, et non sur papier pelure, mesurant de préférence 21,5 × 28 cm (8,5 × 11 pouces), laissant toujours une marge d'au moins 2,5 cm. Si possible, employez un papier avec lignes numérotées en marge.

Tout le manuscrit, y compris tableaux, légendes de figures, renvois et références bibliographiques, devra être dactylographié à double interligne. Ne soulignez que les mots qui devront être imprimés en italique. Mettez en retrait la première ligne de chaque paragraphe du texte et de chaque renvoi.

Dans les titres et les en-têtes, n'employez la majuscule que pour le premier mot et les noms propres. Pour les petites majuscules, employez les miniscules du dactylographe.

Indiquez tous les renvois du texte par des chiffres arabes suscrits. Numérotez les renvois consécutivement par tout le texte, à commencer par ceux de la page titre. Placez chaque renvoi directement sous sa référence, le séparant du texte par des lignes horizontales.

La première page ne doit contenir que le titre de la publication, ne nom et l'affiliation des auteurs, les renvois appropriés et le titre courant (voir Appendice A). Dactylographiez le résumé sur une page séparée (voir Appendice B). Numérotez chaque page, à commencer par la page titre, et y compris celles qui contiennent les tableaux et la légende des figures.

Voyez à ce que l'auteur vérifie le manuscrit final, et soumettez la première copie et ainsi que deux copies lisibles au bureau du Directeur de la publication.

Tableaux. Consultez une copie du *Journal* pour la composition des tableaux (voir Appendice C).

Portez une attention particulière à ce qui suit au sujet des *tableaux numérotés*.

Dactylographiez chaque tableau sur feuille séparée, vous servant de papier sans lignes numérotées.

Numérotez les tableaux en chiffres arabes.

Tracez des lignes horizontales au-dessus et au-dessous des en-têtes et au-dessous des colonnes, rarement ailleurs; ne tracez jamais de lignes verticales; laissez plutôt des espaces supplémentaires.

Indiquez les renvois dans les tableaux par les minuscules suscrites et placez les renvois au bas du tableau.

Placez les tableaux à la suite des références bibliographiques.

A l'endroit où le tableau est mentionné pour la première fois, indiquez dans la marge "Tableau — près d'ici."

Remarquez que les *tableaux dans le texte* ne sont pas numérotés, sont dactylographiés avec le texte et ne requièrent que rarement des lignes horizontales (voir Appendice C).

Figures: Envoyez avec le manuscrit un reproduction photographique (21,5 × 28 cm ou moins) pour chaque illustration. Dactylographiez le nom de l'auteur et le numéro de la figure sur une lisière de papier que vous collerez au dos. N'écrivez pas à la main ou à la machine sur la photographie même. En plus, dactylographiez les légendes, dans l'ordre, sur feuille séparée, intitulée "Légendes des figures." Intercalez cette feuille à la suite du texte.

A l'endroit où chaque figure est mentionnée pour la première fois, inscrivez en marge "Fig. — près d'ici."

Equations, formules et expressions mathématiques: Laissez trois espaces au-dessus et au-dessous des lignes renfermant des chiffres ou des lettres suscrits et souscrits, ou encore au-dessus et au-dessous d'équations et de formules. Placez chaque composante des différentes expressions dans la position qui lui est propre (voir Appendice D).

Indiquez clairement tous les symboles. Epelez en marge les lettres grecques, la première fois qu'elles apparaissent. Faites une distinction entre la lettre *l* et le chiffre *un*, et entre la majuscule *O* et le chiffre *zéro*. Insérez de la même façon toute autre note explicative.

Références: Vérifiez le texte afin de vous assurer que toutes les références apparaissant dans la liste bibliographique sont bien mentionnées dans le texte. Dactylographiez à double interligne dans le style en usage dans le *Journal* (voir Appendice E). Les noms de revues sont abrégés suivants les *Biological Abstracts*; en cas de doute, écrivez le nom au long.

Orthographe: Une liste d'environ 100 mots communément employés dans les périodiques sur les pêches est donnée en Appendice F.

Appendices: On peut se procurer une copie des Appendices A à F sur demande au bureau du Directeur de la publication.

MARINE SCIENCES PAPER 16
(*Also*, GEOLOGICAL SURVEY OF CANADA PAPER 75–9)

The Gravity and Magnetic Fields of Atlantic Offshore Canada

RICHARD T. HAWORTH AND J. BRIAN MACINTYRE

Gravity and magnetic field data collected along approximately 150,000 km of closely spaced ship's tracks off the Atlantic coast of Canada have been compiled at a scale of 1: 1,000,000 and set against a background of data collected on a more regional scale. The maps reflect two major flexed lineations. In the west, the Appalachian front is flexed from Gaspé through the Gulf of St. Lawrence to western Newfoundland. In the east, geophysical trends across the Avalon Platform of Newfoundland are shown to be part of major flexed lineations extending from the Northeast Newfoundland Shelf towards the southern edge of the Grand Banks. The flexures possibly result from Paleozoic continental collision. Gravity anomalies on the Grand Banks define the limit of continental crust, and suggest extensive subsidence of that crust northeast of Newfoundland.

Les auteurs ont compilé, à échelle de 1: 1,000,000, les données sur les champs gravitationnel et magnétique recueillies sur environ 150,000 km de parcours rapprochés de navires au large de la côte canadienne de l'Atlantique, et les ont comparées à des données de fond recueillies à échelle plus régionale. Les cartes révèlent la présence de deux flexures majeures des lignes. A l'ouest, le front appalachien présente une flexure à partir de Gaspé, à travers le golfe Saint-Laurent, jusqu'à l'ouest de Terre-Neuve. À l'est, les tendances géophysiques traversant la plate-forme d'Avalon de Terre-Neuve s'avèrent partie de flexures majeures qui vont du nord-est du plateau terre-neuvien à l'accore méridionale des Grands bancs. Les flexures sont probablement le résultat d'une collision continentale. Des anomalies gravitationnelles sur les Grands bancs définissent la limite de la croûte continentale et suggèrent un effondrement important de cette croûte au nord-est de Terre-Neuve.

(1975, 22 p., 4 maps in pocket; Canada $3.00, other countries $3.60)

To obtain the publications listed above, at the prices indicated, write to:

Information Canada
171 Slater Street
Ottawa, Canada K1A 0S9

Please make cheques and money orders payable to the Receiver General for Canada. Advance payment is required.

On peut se procurer les publications ci-dessus, au prix indiqué, en s'adressant directement à:

Information Canada
171, rue Slater
Ottawa, Canada K1A 0S9

Payables à l'avance. Faire les chèques et les mandats payables à l'ordre du Receveur général du Canada.

Miscellaneous Special Publications/Publications diverses spéciales

22 The algal bowl: lakes and man
J. R. VALLENTYNE
(Reprinted 1975, 186 p., cat. no. Fs 4-31/22; Canada $3.75, other countries $4.50)
Available from: Information Canada, 171 Slater St., Ottawa, Ont. K1A 0S9

23 Methods for the detection of certain pathogens of salmonid fishes/Méthodes de détection de certains agents pathogènes chez les salmonidés
D. C. GILLESPIE, T. P. T. EVELYN, C. FRANTSI, R. M. MACKELVIE, AND/ET N. NEUFELD
(1974, 19 p./21 p., cat. no. Fs 4-31/23; Free/Gratis)
Available from: Information Canada, 171 Slater St., Ottawa, Ont. K1A 0S9

24 Fishes of Canada's National Capital Region/Poissons de la région de la capitale du Canada
D. E. MCALLISTER AND/ET B. W. COAD
(1974, 203 p., cat. no. NM 92-43/1974; Canada $4.00)
Available from: National Museums of Canada, Marketing Services Division, 491 Bank St., Ottawa, Ont.

25 The chemical analysis of fresh water
M. P. STAINTON, M. J. CAPEL, AND F. A. J. ARMSTRONG
(1974, 120 p.; Free)
Available from: Department of the Environment, Fisheries and Marine Service, Freshwater Institute, 501 University Crescent, Winnipeg, Man. R3T 2N6

26 The seashore life of the Gulf Islands
(1975. Pamphlet–poster; Free)
Available from: Department of the Environment, Fisheries and Marine Service, Pacific Biological Station, Nanaimo, B.C. V9R 5K6

27 A practical guide to the anatomy and physiology of Pacific salmon
L. S. SMITH AND G. R. BELL
(1975, 14 p., cat. no. Fs 4-31/27; Canada $2.00, other countries $2.40)
Available from: Information Canada, 171 Slater St., Ottawa, Ont. K1A 0S9

28 Trieste — water levels 1952–1971: a study of the tide, mean level, and seiche activity
G. GODIN AND L. TROTTI
(1975, 24 p., 9 illustrations in pocket (microfiche), cat. no. Fs 4-31/28; Canada $3.00, other countries $3.60)
Available from: Information Canada, 171 Slater St., Ottawa, Ont. K1A 0S9

Development of Design Criteria for Wastewater Treatment Processes

March 28–April 2, 1976

BIOLOGICAL WASTE TREATMENT — March 28–31, 1976
PHYSICAL–CHEMICAL TREATMENT — April 1–2, 1976

REGISTRATION FEE: Biological Waste Treatment — $225
Physical–Chemical Treatment — $175
Both Programs — $350
Fee includes all preprinted material.

OBJECTIVES — This seminar will explore the laboratory and experimental procedures necessary to develop process design data for the biological treatment and physical–chemical treatment of municipal and industrial wastewaters. Laboratory equipment and instrumentation used for experimental programs will be demonstrated and discussed. The correlation and handling of laboratory and pilot plant data and the development of computer programs for process optimization will be presented.

SPONSOR — This seminar is sponsored by the Environmental and Water Resources Engineering Department and the Environmental Associates Program at Vanderbilt University. The seminar will be held at the Hyatt Regency, Nashville, Tennessee.

For more information write:

Prof. W. Wesley Eckenfelder, Jr.
Vanderbilt University
Box 6222, Sta. B
Nashville, Tenn. 37235, USA

Élaboration de Critères S'appliquant à la Conception de Techniques de Traitement des Eaux Usées

Du 28 mars au 2 avril 1976

ÉPURATION BIOLOGIQUE — du 28 au 31 mars 1976
TRAITEMENT PHYSICO–CHIMIQUE — les 1er et 2 avril 1976

FRAIS D'ENREGISTREMENT: Épuration biologique — $225
Traitement physico–chimique — $175
Programme double — $350
Les frais s'appliquent à tout le matériel imprimé à l'avance.

BUTS — Le présent séminaire traitera des techniques de laboratoire et des méthodes expérimentales nécessaires à la conception de procédés de traitement biologique et physico–chimique des eaux usées municipales et industrielles. Le matériel et les instruments expérimentaux de laboratoire feront l'objet de démonstrations et de discussions. On traitera aussi de la corrélation et du traitement des données recueillies en laboratoire et en unité pilote, de même que de la mise au point de programmes d'ordinateur en vue de l'optimalisation des méthodes de traitement.

RESPONSABLE — Le présent séminaire et été organisé par l'Environmental and Water Ressources Engineering Department et par les responsables de l'Environmental Associates Program, de l'université Vanderbilt. Il aura lieu au Hyatt Regency, Nashville (Tennessee).

Pour de plus amples renseignements, veuillez communiquer avec:

W. Wesley Eckenfelder Jr.
Vanderbilt University
Box 6222, Sta. B.
Nashville, Tenn. 37235, USA

Book Review/Compte rendu

Marine Science Communications — basic and applied (D. W. Hood [ed.]) **M. Waldichuk** 346

Books Received/Livres reçus 347
Coming next month/À paraître le mois prochain 348
Guide for authors and typists/Guide des auteurs et Guide pour les secrétaires d'auteurs *i–v*

© Information Canada, Ottawa, 1976

Journal of the Fisheries Research Board of Canada

Journal de l'Office des recherches sur les pêcheries du Canada

JFRBAK33(2)197–348(1976)

Volume 33, No. 2, February 1976

Volume 33, n° 2, février 1976

Preferred temperatures of F_3 to F_5 hybrids of *Salvelinus fontinalis* × *S. namaycush*
C. I. Goddard and J. S. Tait 197–202

Acute toxicity of sodium chloride, pentachlorophenol, Guthion®, and hexavalent chromium to fathead minnows (*Pimephales promelas*) and goldfish (*Carassius auratus*)
I. R. Adelman, L. L. Smith Jr., and G. D. Siesennop 203–208

Fathead minnows (*Pimephales promelas*) and goldfish (*Carassius auratus*) as standard fish in bioassays and their reaction to potential reference toxicants
I. R. Adelman and L. L. Smith Jr. 209–214

Effects of antibacterial agents on nitrification in an aquatic recirculating system
M. T. Collins, J. B. Gratzek, D. L. Dawe, and T. G. Nemetz 215–218

Primary production, extracellular release, and heterotrophy in two lakes in the ELA, northwestern Ontario
C. Nalewajko and D. W. Schindler 219–226

Ecology of Chironomidae (Diptera) in a polar lake
H. E. Welch 227–247

A bioenergetics-based model for pollutant accumulation by fish. Simulation of PCB and methylmercury residue levels in Ottawa River yellow perch (*Perca flavescens*)
R. J. Norstrom, A. E. McKinnon, and A. S. W. deFreitas 248–267

Notes

δ-amino levulinic acid dehydratase activity of fish blood as an indicator of a harmful exposure to lead
P. V. Hodson 268–271

Metazoan parasites of Arctic char (*Salvelinus alpinus*) from the north slope of Canada and Alaska
D. R. Mudry and P. J. McCart 271–275

Relation between yield and fishing mortality for Ricker's yield equation
A. L. Jensen 275–277

Homing behavior and population stratification in central Puget Sound English sole (*Parophrys vetulus*)
D. E. Day 278–282

Role of rearing experience in gravel substrate selection by juvenile rainbow trout, *Salmo gairdneri*
H. R. MacCrimmon and C. M. Hawkins 282–284

Changes in some hematological characteristics of coho salmon (*Oncorhynchus kisutch*) in response to acute exposure to dehydroabietic acid (DHAA) at different exercise levels
G. K. Iwama, G. L. Greer, and P. A. Larkin 285–289

Overhead-light intensity and vertical positioning of the walleye, *Stizostedion vitreum vitreum*
E. Scherer 289–292

Low thermal responsiveness in the bluegill, *Lepomis macrochirus*
T. L. Beitinger and J. J. Magnuson 293–295

Perspectives

Natura Naturans: A Symposium on the Fry Paradigm

Introduction
A. H. Lawrie and S. R. Kerr 296–299

Selected Papers

Some concepts and descriptions of physiological tolerance: rate–temperature curves of poikilotherms as transects of response surfaces
D. F. Alderdice 299–307

Scope for metabolism and growth of sockeye salmon, *Oncorhynchus nerka*, and some related energetics
J. R. Brett 307–313

Predation, yield, and ecological efficiency in aquatic food chains
L. M. Dickie 313–316

Selective breeding and hybridization in fisheries management
P. Ihssen 316–321

A new approach to fisheries management and F. E. J. Fry's role in its development
K. H. Loftus 321–325

Initiation of sea lamprey (*Petromyzon marinus*) control
W. M. Sprules 326–329

Ecological analysis and the Fry paradigm
S. R. Kerr 329–335

Comments

Selected Excerpts from Symposium Discussion Periods 336–339

Acknowledgments 339

Profile of F. E. J. Fry 340–344

List of Participants 344–345

(Continued inside back)